1995

The Role of Fecal Pellets in the Flux of Carbon to the Sea Floor on a River-Influenced Continental Shelf Subject to Hypoxia.

Naureen Aziz Qureshi
Louisiana State University and Agricultural & Mechanical College

THE ROLE OF FECAL PELLETS IN THE FLUX OF CARBON TO THE SEA FLOOR ON A RIVER-INFLUENCED CONTINENTAL SHELF SUBJECT TO HYPOXIA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
Naureen Aziz Qureshi
B.S., University of Karachi, 1974
M.S., University of Karachi, 1977
MPhil., University of Karachi, 1983
May, 1995

To my parents

Aziz Akhtar Qureshi
and
Hamida A. Qureshi

with much love
for always encouraging me in my quest for knowledge

ACKNOWLEDGMENTS

I would like to thank all the people who contributed in various ways to this dissertation and helped me to achieve my goal. First and foremost I would like to thank my major professor, Dr. Nancy N. Rabalais, for her guidance, patience, and unstinting help throughout my dissertation. I thank all the other members of my committee, Drs. R. Eugene Turner, Quay Dortch, William J. Wiseman, Jr., and Frank M. Truesdale. I also thank Dr. John W. Fleeger, the dean's representative on my committee. Each made unique and valuable contributions to my training and to the dissertation. Nancy, Quay, and Gene introduced me to the methodological tools, and application of these methods for scientific inquiry. Their thoughtful discourses, thorough comments and encouragement improved the quality of the dissertation.

My special thanks to Dr. Dubravko Justic' for the friendly and helpful discussions about the processes and understanding of the system, and Jessica Kastler for kindly going through my first drafts and being in many instances a good listener.

I thank Dr. Barry Moser of the Department of Experimental Statistics for his insights on statistical analyses; and Sidina-ould-Dadah and Dr. Glenn Garson, DOCS students, for their informal discussions that helped me make decisions during the data analyses.

This study was supported by research awards from the National Oceanic and Atmospheric Administration, Nutrient Enhanced Coastal Ocean Productivity program, of which this research was a portion of the studies of Drs. N. N. Rabalais, Q. Dortch and R. E. Turner on the flux of materials from the surface waters to the seabed in the zone of hypoxia; the NOAA National Undersea Research Center grants to N. N. Rabalais for mid-summer cruises in 1991 and 1992; and a U.S. Minerals Management Service,

Louisiana Universities Marine Consortium (LUMCON), University Research Initiative grant to N. N. Rabalais.

I would like to thank the LUMCON Foundation, Inc. for a graduate student research award, and the USAID for the research allowance that provided additional financial support towards this research.

I would like to acknowledge the financial support of USAID (United States Agency for International Development) scholarship, the Department of Oceanography and Coastal Sciences, Dr. Rabalais' research grants, and my brother, Tariq A. Qureshi.

I thank the following for their assistance in the field and in the laboratory: Nancy Rabalais and her dive team, especially Lorene Smith, Ben Cole (for data management and boat operations), and Jim Lee as well as the captains and crews of the R/V *Pelican* and the R/V *Acadiana.* Much of this research was conducted at LUMCON facilities, and help from all the LUMCONers is also acknowledged.

I would like to thank all the DOCS students at 'the Stadium' who helped me at different stages and in various ways, especially Jessica Kastler, Sadina-ould-Dadah, and Numair Latif. I also thank my friends in Pakistan and elsewhere for their encouragement and emotional support.

Special thanks to Evelyn and Dr. James Thoms III, who always welcomed me and helped me throughout my stay, especially for letting me stay at their apartment for the last six months of my work.

My special thanks to my family (parents, brothers and sisters) here in the U.S. and in Pakistan for their unwavering love and support that carried me through all the difficult periods.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The Louisiana continental shelf near the Mississippi and Atchfalaya River deltas is a stratified and highly productive coastal system characterized by the largest hypoxic (dissolved oxygen < 2 mg l^{-1}) zone in the western Atlantic Ocean. Carbon export from surface waters in the form of sedimenting zooplankton fecal pellets was examined to determine its importance in the formation and maintenance of oxygen deficiency in the bottom waters.

Two sediment traps (5-6 and 15 m) were deployed in 1991 and 1992 in 20 m water depth within an area of chronic and seasonally severe hypoxia. I determined the fecal pellet number and carbon flux, and total carbon flux from the surface waters, the percent primary production exported as fecal pellets, and the potential for fluxed fecal pellet carbon to support bottom water hypoxia. I also quantitatively sampled the water column at discrete depths for fecal pellets and zooplankton to determine potential source organisms and their seasonal, diel and spatial variation.

The highest densities of total organisms, copepods and copepod nauplii occurred during March and April (1992), when chlorophyll *a* concentrations in surface waters were highest, and decreased in summer and fall. The abundance of fecal pellets was positively correlated with total organisms, copepods and copepod nauplii: the likely source of fecal pellets.

The fluxes of total particulate material, organic carbon, organic nitrogen, fecal pellet carbon and phytoplankton carbon varied similarly between seasons, and was lowest in summer and highest in the spring. The fluxes were greater in 1991 than in 1992. Seasonal variations in fecal pellet number and carbon flux were positively correlated with indicators of high surface water productivity in 1991, but not in 1992.

The flux of fecal pellets from surface to bottom waters accounted for 55% of the particulate material exported vertically, exceeded phytoplankton carbon fluxes, and was high enough to deplete the bottom water oxygen reserves in spring.

The results support the hypothesis that the development of summer hypoxia is associated with the decomposition of organic matter accumulated in spring primarily by the sedimentation of phytoplankton bloom via fecal pellets, and not as intact phytoplankton cells.

CHAPTER 1

INTRODUCTION

BACKGROUND FOR RESEARCH

The increased incidence of oxygen depleted bottom waters in coastal waters worldwide is related to increasing eutrophication, especially at the terminus of major rivers that have changed dramatically in their nutrient and/or organic loadings (Rabalais et al. 1991, Turner & Rabalais 1994, Justic' et al. 1994a). Oxygen deficient bottom waters are operationally defined as hypoxic at dissolved oxygen levels of < 2 mg O_2 l^{-1}. The bottom water hypoxic zone in the northern Gulf of Mexico extends up to 16,500 km^2 on the inner continental shelf, from the Mississippi River delta to the northeastern Texas shelf, and is the largest, most severe and most persistent in the western Atlantic Ocean (Rabalais et al. 1991, 1994a). Hypoxic bottom waters occur primarily from April to October and are most severe, persistent and extensive from June to August. The yearly variation in the distribution of hypoxia (Fig. 1.1) is related to variations in the magnitude and timing of the Mississippi River discharge (Fig. 1.2), large-scale circulation patterns, solar heating and wind events. The formation of hypoxic bottom water in this system depends on strong density stratification and high inputs of organic matter (Rabalais et al. 1991, 1992).

The Louisiana inner continental shelf is influenced by the effluents of two major rivers, the Mississippi and Atchafalaya, of which the Mississippi River discharge amounts to as much as 65% of the total inflow of the entire drainage basin (Moody 1967). Much of the fresh water discharged by the Mississippi and Atchafalaya is retained on the inner shelf by the winds and currents, and a vertically stable stratified system predominates most of the year. This density stratification reduces vertical

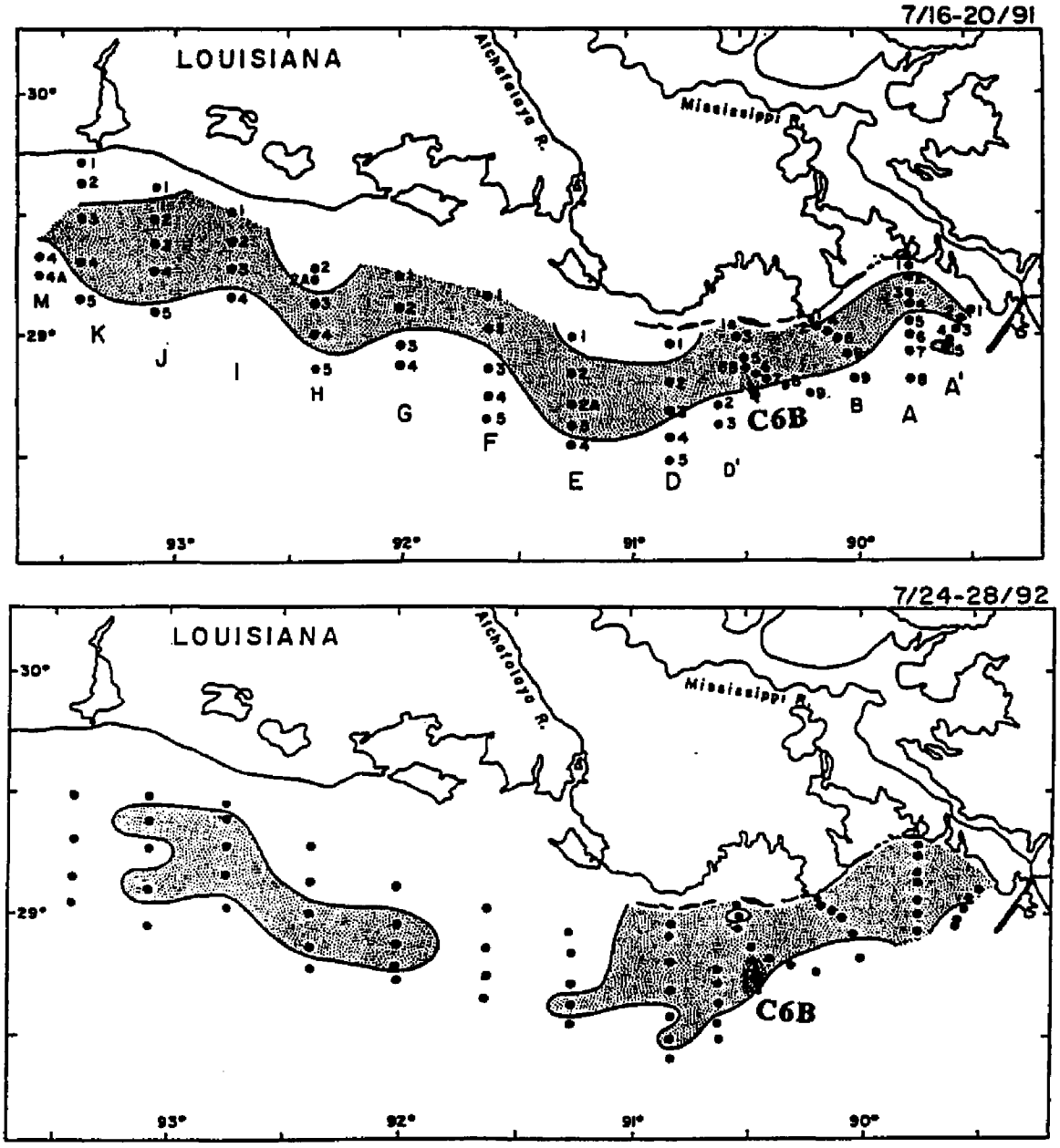


Figure 1.1. Distribution of dissolved oxygen concentrations ≤ 2 mg l^{-1} in near bottom waters in 1991 (upper panel) and 1992 (lower panel).

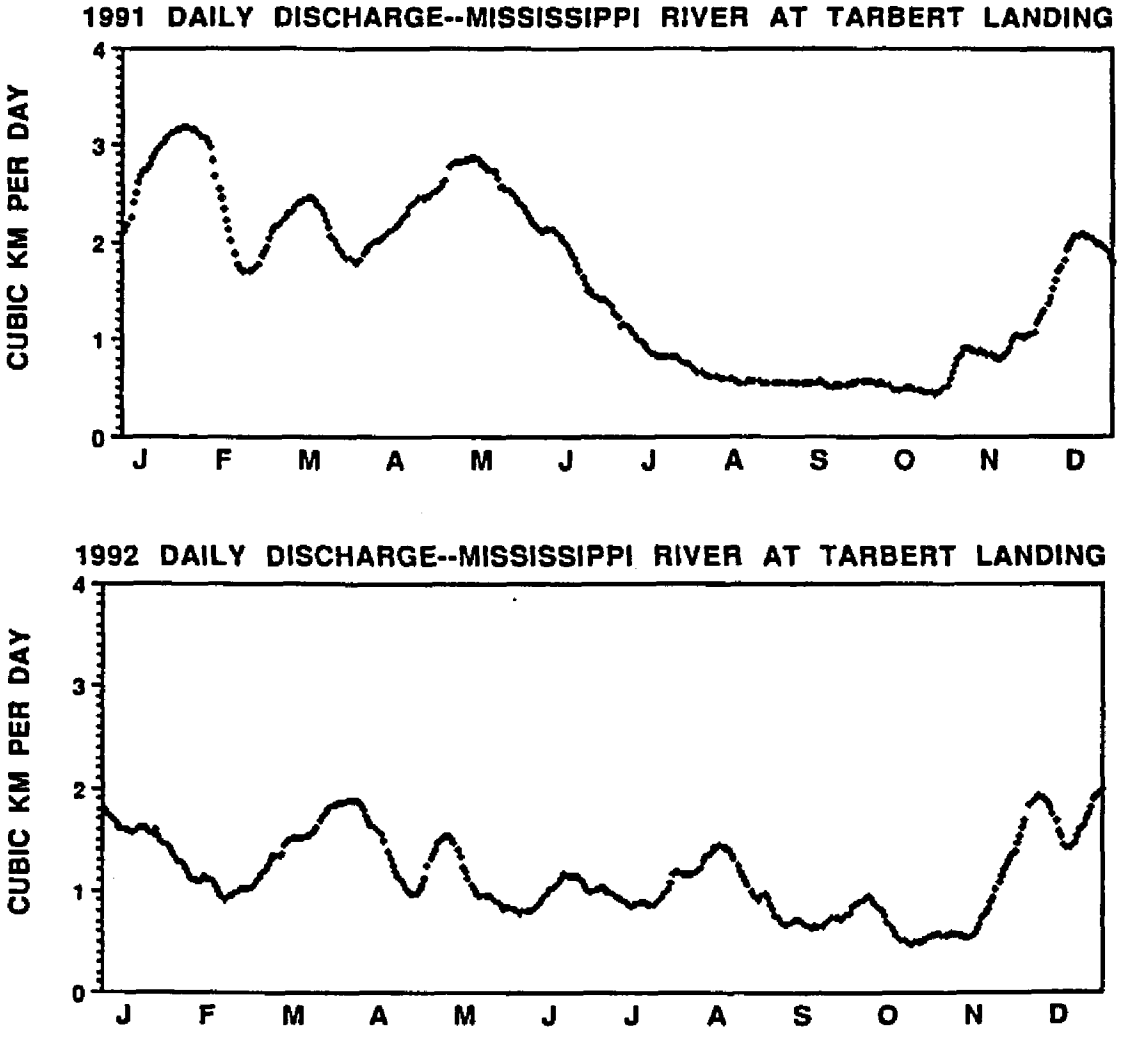


Figure 1.2. Daily Mississippi River discharge in 1991 (upper panel) and in 1992 (lower panel) at Tarbert Landing, Mississippi.

diffusion and isolates oxygen depleted bottom waters from resupply of oxygen from the well-oxygenated surface layers.

In addition to density stratification, oxygen consumption rates from respiration by heterotrophic organisms and from bacterial degradation of oxidizable carbon, which are higher than the rates of resupply, contribute to the observed hypoxia. Organic loading to the seabed and the lower water column is necessary for hypoxia to occur. Determining the source of the organic matter is essential to understanding the factors controlling hypoxia. Initially, the source of carbon fueling hypoxia was hypothesized to be organic material discharged from the Mississippi River (Gallaway 1981). Several studies based on stable carbon isotope ratios indicate marine rather than terrestrial origin of organic matter within a very short distance of the river mouth (Sackett et al. 1965, Gearing et al. 1977, Thayer et al. 1983, Eadie et al. 1994, Turner & Rabalais 1994). Further, there is insufficient oxidizable carbon input from the river to account for the oxygen draw down leading to hypoxia (Boesch 1983).

The effects of hypoxia on the benthic communities are severe and are manifested in reduced abundance and species richness (Murrell & Fleeger 1989, Boesch & Rabalais 1991, Harper et al. 1981, 1991). Hypoxia may also affect fisheries resources in the Gulf of Mexico for which various life history stages depend on habitats of the inner shelf, especially during summer when hypoxia is often severe and widespread (Pavela et al. 1983, Leming & Stuntz 1984, Renaud 1986, N. N. Rabalais pers. comm.).

The influence of the Mississippi and Atchafalaya rivers on the biological processes of the continental shelf is reflected in high primary production near the Mississippi River delta, which averages 329 g C m^{-2} yr^{-1} in the plume region (Lohrenz et al. 1990) and 290 g C m^{-2} yr^{-1} on the southeastern shelf (Sklar & Turner 1981). Variations in primary production and chlorophyll biomass in the plume are partly explained by changes in light and nutrient availability and changes in physiological variables resulting in changes in species composition of phytoplankton (Lohrenz et al.

1990, 1994). Dramatic changes in nutrient concentrations, loadings, and ratios of the flows of the Mississippi and Atchafalaya rivers have occurred since the mid-1950s with doublings of nitrate and total phosphorus and a reduction by 50% in silicate (Turner & Rabalais 1991, 1994). Shifts in the stoichiometric nutrient balance in the Mississippi River plume, with increased potential for silica limitation relative to nitrogen and phosphorus limitation (Justic' et al. 1994a, b, Turner & Rabalais 1991, 1994, Dortch & Whitledge 1992), suggest a potential for increased productivity, as well as a shift in the composition of phytoplankton communities and higher trophic levels (e.g. zooplankton communities). These complex interactions may ultimately affect the overall trophic structure, regeneration of nutrients, remineralization of carbon and the fate of carbon on the continental shelf adjacent to the altered nutrient fluxes. Turner and Rabalais (1994) demonstrated increased eutrophication of the continental shelf in the Mississippi River bight coincidental with increases in nitrate loadings from the Mississippi River.

The transport of organic carbon to depth as a fraction of primary production depends on the fraction of settling particles as well as on their subsequent consumption and modification (Noji 1991, Aksnes & Wassmann 1993). The structure and the function of the particular food webs play important roles in export potential. My research was based on the hypothesis that zooplankton fecal pellets, produced by zooplankton grazing on primary productivity stimulated by high nutrient inputs, are the primary source of carbon flux to the inner continental shelf seabed influenced by the Mississippi River flow and subject to hypoxia and that the carbon fluxed via fecal pellets is sufficient to cause oxygen depletion.

FECAL PELLET FLUX AND FLUX OF ORGANIC MATERIAL

Many factors affect the flux of the surface organic production to the seabed on the southeastern Louisiana continental shelf. Large-scale circulation patterns may advect surficial plume waters to great distances from the immediate river delta

(Rabalais et al. 1994b). Carbon fixed by primary production can be processed within the upper mixed layer by zooplankton grazing or by bacterial remineralization. The importance of bacterial remineralization is indicated by high water column respiration rates (Turner & Allen 1982) and high bottom-water respiration rates (Chin-Leo & Benner 1992, Dortch et al. 1994). Positive correlations between community respiration and chlorophyll concentration indicate phytoplankton sinking (as cells or repackaged as fecal pellets) as the source of organic carbon being respired (Turner & Allen 1982). Carbon fixed by primary productivity is either sedimented directly as phytoplankton biomass or is integrated into larger particles by production of fecal pellets and/or aggregate formation. Biogenic particle settling is considered to be responsible for much of the transport of carbon to the sea floor.

Massive and rapid sedimentation of phytoplankton cells following surface blooms has been observed (Smetacek 1980, Peinert et al. 1982, Wassmann 1983, Davies & Payne 1984, Billet et al. 1983). Sedimentation is either enhanced by spore or seed formation (Smetacek 1985) or by formation of mass flocs or aggregates during or after the bloom (Smetacek 1985, Alldredge & Gotschalk 1989, Riebesell 1989), where aggregate formation is a successional aggregation of selected diatom species (Riebesell 1991, Dortch et al. 1992). However, the actual contribution of marine snow to carbon flux is highly variable and can be related to size, abundance, composition, age and origin of the aggregate. Four different types of aggregates, or marine snow, are reported including larvacean houses, diatom flocs, fecal aggregates and aggregates composed primarily of debris and detritus (Alldredge & Gotschalk 1990).

Zooplankton fecal pellets, specifically from copepods and euphausiids, are often considered major vehicles of rapid transport of material to the seafloor (Honjo 1977, 1980, Angel 1984, Smetacek 1985, Honjo & Roman 1978, Dunbar & Berger 1981, Wiebe et al. 1976, , Pilskaln & Honjo 1987, Small et al. 1989). Lohmann (1902) first suggested the geological significance of oceanic fecal pellets as a mechanism of carbon

transport to the sea floor. Zooplankton feeding in the euphotic zone incorporated coccoliths into rapidly settling fecal pellets which deposited and formed deep-sea coccolith oozes. Diatoms and silicoflagelletes have also been found in fecal pellets that were preserved in anoxic sediments (Porter 1984, Haberyan 1985). Honjo (1977) estimated transport of 92% of coccoliths, produced in the euphotic zone in the equatorial Pacific, via rapidly settling fecal pellets to the underlying seafloor.

Studies of chemical signatures also show the importance of fecal pellets in vertical transport of material to the bottom. Nitrogen isotope ratios show low differences in ^{15}N between sedimenting particles and fecal pellets, which suggest a common origin of sinking and suspended particles (Altabet & Small 1988). Vertical flux of certain biolipids also shows a fecal signature at great depths (Corner et al. 1986).

The contribution of carbon flux attributed to zooplankton fecal pellets has been reported from many studies using sediment traps, in both the open ocean (Wiebe et al. 1976, Bishop et al. 1977, Honjo 1977, 1980, Knauer & Martin 1981, Urrere & Knauer 1981, Pilskaln & Honjo 1987, Deuser et al. 1981) and in shallow and coastal areas (Shuman 1978, Smetacek 1980, Dunbar & Berger 1981, Bochdansky & Herndl 1992). These studies show the fecal pellet contribution by weight to vertical flux varies from 1% (Pilskaln & Honjo 1987) to more than 90% (Bathmann et al. 1987) and is a function of seasonal surface production, zooplankton grazing activity, nutrients and depth. The transport of organic carbon to depth as a fraction of primary production depends on the fraction of settling particles as well as on their subsequent consumption and modification (Noji 1991, Aksnes & Wassmann 1993). The structure and the function of the particular food webs play an important role in export potential.

Fecal pellets vary in size and shape, depending on the source organism and the quality and quantity of food resources. Examples are: euphausiid fecal strings (Moore 1931, Bodungen 1986, Clarke et al. 1988), oval pellets of amphipods and ostracods (Bathmann et al. 1991), ellipsoid and cylindrical pellets of copepods (Gowing & Silver

1983, Bathmann et al. 1987, Fowler et al. 1991) and tunicates (Deibel 1990), coils of doliolids and pteropods (Silver & Bruland 1981) and large mats produced by salps (Iseki 1981, Silver & Bruland 1981). These fecal pellet types are considered major vehicles for transport of organic particulate material (Fowler & Small 1972, Hofmann et al. 1981, Lorenzen & Welschmeyer 1983, Fowler et al. 1987). The flux of fecal pellets produced by gelatinous zooplankton (salps, pteropods, doliolids, etc.), however, can be considerably greater and can disproportionately affect the amount of carbon flux, especially during periods of dense population blooms (Bruland & Silver 1981).

The importance of fecal pellets in sedimentation of organic material depends largely on two attributes viz. sinking rates and degradation of fecal pellets. Sinking rates of fecal pellets (in the range of 10^1 to 10^3 m d^{-1}, Madin 1982) depend on the size of fecal pellets, because there are linear relationships between sinking velocity and both particle size and the density of fecal pellets (Deibel 1990, Urban et al. 1992). The quality of food ingested affects the size and density of fecal pellets (Bienfang 1980, Dagg & Walser 1986, Voss 1991, Urban et al. 1992). Fecal pellets containing diatom frustules are more dense (1.17 g cm^{-3}) and sink faster than those composed primarily of flagellates (1.11 g cm^{-3}) (Smayda 1969, Bienfang 1980).

Degradation of fecal pellets increases the residence time of fecal pellets in the water column and, therefore, retards the vertical flux (Peinert et al. 1989, Paffenhofer & Knowles 1979, Lampitt et al. 1990, Noji 1991). Degradation is promoted via various mechanisms such as coprophagy (reingestion of fecal pellets by zooplankton) (Paffenhofer & Knowles 1979), coprorhexy (mechanical breakage of fecal pellets by organisms), and coprochally (loosening of fecal pellets) (Lampitt et al. 1990, Noji 1991).

The carbon flux of sedimenting fecal pellets can also be affected by rapid diffusion (hours to days) of fecal carbon to the dissolved organic carbon pool (Jumars et al. 1989). The loss to the DOC pool can be as great as 90%, and this DOC may fuel

bacterial production that will further promote pelagic microbial recycling of material in the water column (Jumars et al. 1989). Fecal pellets may be colonized by bacteria and protists in the water column (Jacobsen & Azam 1984, Alldredge et al. 1986, Nagasawa & Nemoto 1988). Freshly voided pellets may contain gut bacteria (Andrews et al. 1984) which will then affect fecal pellet degradation and, subsequently, the vertical flux of particulate organic carbon (Poulet et al. 1986).

Degradation of fecal pellets in the water column affects particulate carbon and nitrogen flux. The C:N ratio increases with the degradation of fecal pellets (Head 1992) where C and N decrease by 25% to 50% in 2 to 22 days at 5 °C and 15 °C (Turner 1979, Roy & Poulet 1990). High variability in the initial carbon and nitrogen content of fecal pellets; however, is related to differences in food quality (Morales 1987).

Zooplankton grazing impact is a dominant influence on the export of particulate organic material from the euphotic zone in freshwater and marine environments (Bloesh & Burger 1989, Peinert et al. 1989). Studies in the northern Gulf of Mexico and Mississippi River plume region indicate high zooplankton standing stocks coincident with high phytoplankton biomass. High concentrations of copepod nauplii (> 1000 l^{-1}) are associated with plume waters (Dagg & Whitledge 1991). Higher zooplankton stocks in summer imply higher grazing in summer than in spring or winter (Dagg & Whitledge 1991). The distribution of the zooplankton community, however, varies spatially and with depth (Dagg & Whitledge 1991, Dagg & Ortner 1992, pers. observ.). Copepods contribute more than 80% of the number and half the biomass of the mesozooplankton communities in the eastern Gulf of Mexico (Howey 1976, Hopkins 1982). Temporal and spatial variability of zooplankton communities will likely affect the flux of carbon via fecal pellets.

Fecal pellet flux can be quantitatively and qualitatively influenced by discriminate feeding of zooplankton, selective utilization of ingested particles and their vertical migration. The effect of migration can be particularly important on diel scales

related to feeding activities (Hopkins et al. 1978, Dagg & Walser 1987). Zooplankters pump material to deeper water layers by feeding near the surface and defecating or partly egesting in deeper waters (Emerson & Roff 1987, Longhurst & Harrison 1988). This biological pump contributes significantly to the downward vertical flux of carbon, especially in coastal areas (Noji 1991).

RESEARCH APPROACH AND OBJECTIVES

The overall aim of this study was to examine the contribution of fecal pellets to the total organic carbon flux and their potential to induce hypoxia on the riverine-influenced continental shelf. Two techniques were used for quantitative study of the processes related to particle sedimentation: (1) interception of fluxed particles into moored sediment traps, which gives a time and depth integrated sample, and (2) filtration of sea water (large volumes through various sized meshes usually > 20 μm size fraction) which gives *in situ* concentrations and is a 'snapshot' approach. Both methods present limitations to obtaining unbiased data. Sediment trap samples have problems associated with various physical dimensions, forms and methods of deployment in a time-varying flow field, as well as problems of preservatives, 'swimmers' and sample processing (Knauer & Asper 1989). Data obtained by filtration of sea water is restrained by the amount of water that can be filtered and the bulk of material and size selection bias due to the mesh sizes used. I obtained samples for this study from sediment traps mounted on a permanent instrument mooring (Fig. 1.3), surface water zooplankton tows, and filtration of large volumes of sea water from discrete depths to test different hypotheses as described below.

The temporal variability of fecal pellets and the associated carbon flux to the seabed on the inner continental shelf under the influence of the Mississippi River and subject to conditions of severe bottom water hypoxia are presented in Chapter 2. I predicted that (1) fecal pellet and fecal pellet carbon fluxes were greater in the summer

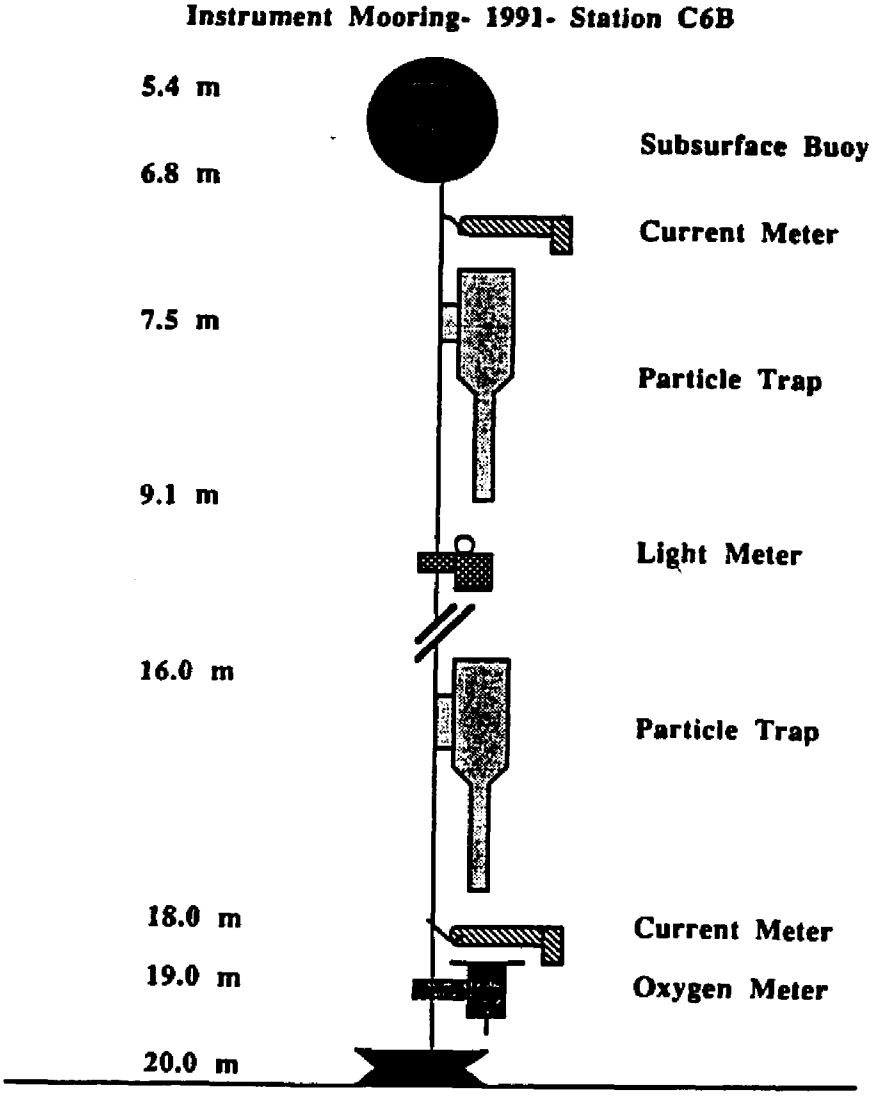


Figure 1.3. Schematic diagram of sediment traps, current meters, light meter and dissolved oxygen meter on the permanent mooring at station C6B during 1991 and 1992.

when more mature zooplankton communities were present, (2) the fecal pellet and carbon flux were higher in the surface waters than below (in the top trap in the euphotic region), and (3) the larger fecal pellets (produced by mesozooplankton) dominated the fecal pellet and fecal pellet carbon fluxes.

The contribution and importance of fecal pellet carbon flux in the export of particulate material and the potential to induce hypoxia is presented in Chapter 3. I determined the temporal variability of the fluxes of particulate matter (total particulate material, particulate organic carbon, particulate organic nitrogen and total pigments) and compared these to the fecal pellet carbon flux. I also compared fecal pellet carbon flux with estimates of phytoplankton carbon flux to determine their relative importance to the total carbon flux, the fraction of estimated surface productivity exported to the seabed by each, and the potential to induce oxygen depletion and contribution to hypoxia. I predicted that (1) fecal pellets were the primary source of carbon fluxed to the seabed on the river-influenced continental shelf, (2) the fecal pellet carbon flux was greater than the phytoplankton carbon flux, (3) the fecal pellet carbon flux was greater in summer than in spring and fall and was higher in the top trap, and (4) the oxidation of the fluxed fecal pellet carbon was sufficient to induce hypoxia in spring which was then sustained through the summer by the stable, stratified water column. I also estimated the fraction of surface water primary production exported by both fecal pellet carbon flux and phytoplankton carbon flux.

The producers of fecal pellets collected in the sediments traps were not known. To identify the potential source organisms, I examined the mesozooplankton community structure, copepod species composition and seasonal variation in the mesozooplankton community in the vicinity of the moored sediment traps (Chapter 4). The inherent assumption in this approach was that the materials collected in the traps were produced in the vicinity of the traps.

I also enumerated the zooplankton community by filtration of sea water from discrete depths (Chapter 5). The objective of this study was to determine the effect of a stratified water column and oxygen depleted bottom waters on the temporal variability and the distribution and abundance of meso- and microzooplankton and fecal pellets at diel and monthly scales, and over a continuum of varying concentrations of bottom waters dissolved oxygen on a broad spatial scale. I also enumerated fecal pellets from these samples to examine the linkage between the meso- and microzooplankton communities and the instantaneous concentrations of fecal pellets (i.e., were the fecal pellets produced by the organisms *in situ* or were they advected into the study area?).

REFERENCES

AKSNES, D. L., AND P. WASSMANN. 1993. Modeling the significance of zooplankton grazing for export production. Limnol. Oceanogr. **38**: 978-985.

ALLDREDGE, A. L., AND C. C. GOTSCHALK. 1989. Direct observations of mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep-Sea Res. **32**: 159-171.

_____, AND C. C. GOTSCHALK. 1990. The relative contribution of marine snow of different origins to biological processes in coastal waters. Continental Shelf Research **10**: 41-58.

_____, J. J. COLE, AND D. A. CARON. 1986. Production of the heterotrophic bacteria inhabiting macroscopic organic aggregates (marine snow) from surface waters. Limnol. Oceanogr. **31**: 68-78.

ALTABET, M. A., AND L. F. SMALL. 1988. Nitrogen isotopic ratios in zooplankton fecal pellets: Nitrogen transformation and flux from the euphotic zone. EOS **69**: 1090-1091.

ANDREWS, C. C., D. M. KARL, L. F. SMALL, AND S. W. FOWLER. 1984. Metabolic activity and bioluminescence of oceanic faecal pellets and sediment trap particles. Nature **307**: 539-541.

ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems. p. 475-516. *In*: M. J. R.Fasham, [ed.], Flow of energy and material in marine ecosystems. NATO Conference series V. Marine Science 13. Plenum.

BATHMANN, U. V., T. T. NOJI, M. VOSS, AND R. PEINERT. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar. Ecol. Prog. Ser. **38**: 45-51.

_____, T. T. NOJI, AND B. VON BODUNGEN. 1991. Sedimentation of pteropods in the Norwegian Sea in autumn. Deep-Sea Res. **38**: 1341-1360.

BIENFANG, P. K. 1980. Herbivore diet affects fecal pellet settling. Can. J. Fish. Aqua. Sci. **37**: 1352-1357.

BILLET, D. S. M., R. S. LAMPITT, A. L. RICE, AND R. F. C. MANTOURA. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature **302**: 520-522.

BISHOP, J. K. B., J. M. EDMOND, D. R. KETTEN, M. P. BACON, AND W. B. SILKER. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. **23**: 511-548.

BLOESCH, J., AND H.-R. BURGER. 1989. Changes in phytoplankton and zooplankton biomass and composition and composition reflected in sedimentation. Limnol. Oceanogr. **34**: 1048-1061.

BOCHDANSKY, A. B., AND G. J. HERNDL. 1992. Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. V. Role of fecal pellets in marine snow. Mar. Ecol. Prog. Ser. **89**: 297-303.

BODUNGEN, B. VON. 1986. Phytoplankton growth and krill grazing during spring in the Bransfield Strait, Antarctica - implications from sediment trap collections. Polar Biol. **6**: 153-160.

BOESCH, D. F. 1983. Implications of oxygen depletion on the continental shelf of the Northern Gulf of Mexico. Coast. Ocean Pollut. Assess. News **2**: 25-28.

_____, AND N. N. RABALAIS. 1991. Effects of hypoxia on continental shelf benthos: Comparisons between the New York Bight and the Northern Gulf of Mexico. p. 27-34. *In* R. V. Tyson and T. H. Pearson [eds.], Modern and ancient continental shelf anoxia. Geological Society Special Publication No. 58, The Geological Society, London.

BRULAND, K. W., AND M. W. SILVER. 1981. Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). Mar. Biol. **63**: 295-300.

CHIN-LEO, G., AND R. BENNER. 1992. Enhanced bacterioplankton production and respiration at intermediate salinities in the Mississippi River plume. Mar. Ecol. Prog. Ser. **87**: 87-103.

CLARKE, A., L. B. QUETIN, AND R. M. ROSS. 1988. Laboratory and field estimates of the rate of fecal pellet production by Antarctic krill. Euphausia superba. Mar. Biol. **98**: 557-563.

CORNER, E. D. S., S. C. M. O'HARA, A. C. NEAL, AND G. EGLINTON. 1986. Copepod fecal pellets and the vertical flux of biolipids. p. 261-321. *In* E. D. S. Corner and S. C. M. O'Hara [eds.], The biological chemistry of marine copepods. Claredon press, Oxford.

DAGG, M. J., AND P. ORTNER. 1992. Mesozooplankton grazing and the fate of carbon in the northern Gulf of Mexico. p. 117-121. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, AND W. E. WALSER. 1986. The effect of food concentration on fecal pellet size in marine copepods. Limnol. Oceanogr. **31**: 1066-1071.

_____, AND _____. 1987. Ingestion, gut passage, and egestion by the copepod Neocalanus plumchrus in the laboratory and in the subarctic Pacific Ocean. Limnol. Oceanogr. **32**: 178-188.

_____, AND T. E. WHITLEDGE. 1991. Concentrations of copepod nauplii associated with the nutrient rich plume of the Mississippi river. Cont. Shelf Res. **11**: 1409-1423.

DAVIES, J. M. AND R. PAYNE. 1984. Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. Mar. Biol. **78**: 315-324.

DEIBEL, D. 1990. Still-water sinking velocity of fecal material from pelagic tunicate *Dolioletta gegenbaursi*. Mar. Ecol. Prog. Ser. **62**: 55-60.

DEUSER, W. G., E. H. ROSS, AND R. F. ANDERSON. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. Deep-Sea Res. **28**: 495-505.

DORTCH, Q., AND T. E. WHITLEDGE. 1992. Does nitrogen or silicon limit phytoplankton production in the Mississippi River plume and nearby regions? Cont. Shelf Res. **12**: 1293-1300.

_____, D. MILSTED, N. N. RABALAIS, S. E. LOHRENZ, D. G. REDALGE, M. J. DAGG, R. E. TURNER, AND T. E. WHITLEDGE. 1992. Role of silicate availability in phytoplankton species composition and the fate of carbon. p. 76-85. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, N. N. RABALAIS, R. E. TURNER, AND G. T. ROWE. 1994. Respiration rates and hypoxia on the Louisiana Shelf. Estuaries **17**: 862-872.

DUNBAR, R. B., AND W. H. BERGER. 1981. Fecal pellet flux to modern bottom sediment of Santa Barbara Basin (California) based on sediment trapping. Geol. Soc. Am. Bull. **92**: 212-218.

EADIE, B. J., B. A. MCKEE, M. B. LANSING, J. A. ROBBINS, S. METZ, AND J. H. TREFRY. 1994. Records of nutrient enhanced coastal ocean productivity in sediments from the Louisiana continental shelf. Estuaries **17**: in press.

EMERSON, C. W., AND J. C. ROFF. 1987. Implications of fecal pellet size and zooplankton behavior to estimates of pelagic-benthic carbon flux. Mar. Ecol. Prog. Ser. **35**: 251-257.

FOWLER, S. W., AND L. F. SMALL. 1972. Sinking rates of euphausiid fecal pellets. Limnol. Oceanogr. **17**: 293-296.

_____, P BUAT-MENARD, Y. YOKOYAMA, S. BALLESTRA, E HOLM, AND H. V. NGUYEN. 1987. Rapid removal of Chernobyl fallout from Mediterranean surface waters by biological activity. Nature **329**: 56-58.

_____, L. F. SMALL, AND J. L. ROSA. 1991. Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter. Oceanol. Acta **14**: 77-85.

GALLAWAY, G. J. 1981. An ecosystem analysis of oil and gas development on the Texas-Louisiana shelf. Biological Services Program Publication FWS/OBS-81/27, U. S. Dept. of Interior, Bureau of Land Management, Fish and Wildlife Service, Washington, D. C. 89 p.

GEARING, P., F. E. PLUCKER, AND P. L. PARKER. 1977. Organic carbon stable isotope ratios of continental margin sediments. Mar. Chem. **5**: 251-266.

GOWING, M. M., AND M. W. SILVER. 1983. Origins and microenvironments of bacteria mediating fecal pellet decomposition in the sea. Mar. Biol. **73**: 7-16.

HABERYAN, K. A. 1985. The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika. Limonol. Oceanogr. **30**: 1010-1023.

HARPER, JR., D. E., L. D. MCKINNEY, R. R. SALZER, AND R. J. CASE. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effect on the benthic biota. Contrib. Mar. Sci. **24**: 53-79.

_____, _____, J. M. NANCE, AND R. SALZER. 1991. Recovery responses of two benthic assemblages following an acute hypoxia event on the Texas continental shelf, northwestern Gulf of Mexico. p. 49-64. *In* R. V. Tyson and T. H. Pearson [eds.], Modern and Acient Continental Shelf Anoxia. Geological Society Special Publication NO. **58**. The Geological Society.

HEAD, E. J. H. 1992. Comparison of the chemical composition of particulate material andcopepod faecal pellets at stations off the coast of Labrador and in the Gulf of St. Lawrence. Mar. Biol. **112**: 593-600.

HOFMANN, E. E., J. M. KLINCK, AND G.-A. PAFFENHOFER. 1981. Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. Mar. Biol. **61**: 327-335.

HONJO, S. 1977. Biogenic carbonate particles in the ocean: Do they dissolve in the water column? p. 269-294. *In* N. R. Andersen and A. A. Malahoff (eds.) The fate of fossil fuel CO_2. Plenum.

_____. 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. Mar. Res. **38**: 53-97.

_____, AND M. R. ROMAN. 1978. Marine copepod fecal pellets: production, preservation and sedimentation. J. Mar. Res. **36**: 45-57.

HOPKINS, T. L. 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. Deep-Sea Res. **29**: 1069-1083.

HOPKINS, C. C. E., S. FALK-PETERSEN, K. TANDE, AND H. C. EILERTSEN. 1978. A preliminary study of zooplankton sound scattering layers in Balsfjorden: structure, energetics, and migrations. Sarsia **63**: 255-264.

HOWEY, T. W. 1976. Zooplankton of the Gulf of Mexico: Distribution of displacement volume, occurrence of systematic groups, abundance and diversity among copepods. Ph.D. Dissertation. Louisiana State University, Baton Rouge.

ISEKI, K. 1981. Particulate organic matter transport to the deep sea by salp fecal pellets. Mar. Ecol. Prog. Ser. **5**: 55-60.

JACOBSEN, T. R., AND F. AZAM. 1984. Role of bacteria in copepod fecal pellet decomposition, colonization, growth rates and mineralization. Bull. Mar. Sci. **35**:495-502.

JUMARS, P. A., D. PENRY, J. A. BAROSS, M. J. PERRY, AND B. FROST. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res. **36**: 483-495.

JUSTIC', D., N. N. RABALAIS, R. E. TURNER, AND W. J. WISEMAN JR. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. Mar. Pollut. Bull. **26**: 184-189.

_____, _____, AND _____. 1994a.Stoichiometric nutrient balances and origin of coastal eutrophication. Mar. Pollut. Bull. in press.

_____, _____, AND _____. 1994b. Riverborne nutrients, hypoxia and coastal ecosystem evolution: Biological responses to long-term changes in nutrient loads carried by the Po and Mississippi Rivers. *In* K. Dyer [ed.], Changes in fluxes in estuaries: Implications from science to management. Proceedings, ECSA22 Symposium, Joint ESCA/ERF Conference, International Symposium Series, Olsen & Olsen, in press.

KNAUER, G. A., AND V. ASPER [EDS.]. 1989. Sediment trap technology and sampling. U. S. GOFS Planning Rep. 10.

_____, AND J. H. MARTIN. 1981. Primary production and carbon-nitrogen fluxes in the upper 1500 m of the northeast Pacific. Limnol. Oceanogr. **26**: 97-108.

LAMPITT, R. S., T. NOJI, AND R. VON BONUNGEN. 1990. What happens to zooplankton faecal pellets? Implications for material flux. Mar. Biol.**104**: 15-23.

LEMING, T. D., AND W. E. STUNTZ. 1984. Zones of coastal hypoxia revealed by satellite scanning have implications for strategic fishing. Nature **310**: 136-138.

LOHMANN, H. 1902. Die coccolithophoridae, eine Monograohie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeeratftriebs. Arch. Protistenka 1: 89-165.

LOHRENZ, S. E., M. J. DAGG, AND T. E. WHITLEDGE. 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Cont. Shelf Res. **10**: 639-664.

_____, G. L. FAHNENSTEIL, AND D. G. REDALGE. 1994. Spatial and temporal variations of photosynthetic parameters in relation to environmental conditions in northern Gulf of Mexico coastal waters. Estuaries **17**: in press.

LONGHURST, A. G., AND W. G. HARRISON. 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. **35**: 881-889.

LORENZEN, C. J., AND N. A. WELSCHMEYER. 1983. The in situ sinking rates of herbivore fecal pellets. J. Plank. Res. **5**: 929-933.

MADIN, L. P. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar. Biol. **67**: 39-45.

MOODY, C. L. 1967. Gulf of Mexico distributive provinces. Am. Assoc. Petro. Geol. Bull. **51**: 179-199.

MOORE, H. B. 1931. The specific identification of faecal pellets. J. Mar. Biol. Assoc.U.K. **17**: 359-365.

MORALES, C. E. 1987. Carbon and nitrogen content of copepod faecal pellets: effect of food concentration and feeding behavior. Mar. Ecol. Prog. Ser. **36**: 107-114.

MURRELL, M. C., AND J. W. FLEEGER. 1989. Meiofauna abundance on the Gulf of Mexico continental shelf affected by hypoxia. Cont. Shelf Res. **9**: 1049-1062.

NAGASAWA, S., AND T. NEMOTO. 1988. Presence of bacteria in guts of marine crustaceans and on their fecal pellets. J. Plank. Res. **10**: 559-564.

NOJI, T. T. 1991. The influence of macrozooplankton on vertical particulate flux. Sarsia **76**: 1-9.

PAFFENHOFER, G. A., AND S.C. KNOWLES. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. J. Mar. Res. **37**: 35-49.

PAVELA, J. S., J. L. ROSS, AND M. E. CHITTENDEN, JR. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. Northeast Gulf Sci. **6**: 167-173.

PEINERT, R., A. SAURE, P. STEGEMANN, G. STIENEN, H. HAARDT, AND V. SMETACEK. 1982. Dynamics of primary production and sedimentation in a coastal ecosystem. Neth. J. Sea Res. **16**: 276-289.

_____, B. VON BODUNGEN, AND V. S. SMETACEK. 1989. Food web structure and loss rate. p. 35-48. *In* W. H. Berger, V. S. Smetacek and G. Wefer [eds.], Productivity of the ocean: Present and past. Wiley & Sons.

PILSKALN, C. H., AND S. HONJO. 1987. The fecal pellets fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles **1**: 31-48.

PORTER, K. G. 1984. Alternate fate of planktonic detritus: organic deposition and the geological record. Bull. Mar. Sci. **35**: 587-600.

POULET, S. A., R. P. HARRIS, V. MARTIN-JEZEQUEL, J. MOAL, AND J. -F. SAMAIN. 1986. Free amino acids in copepod faecal pellets. Oceanol. Acta **9**: 191-197.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. p. 35-47. *In* R. V.Tyson, and T. H. Pearson [eds.], Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. **58**.

_____, _____, AND _____. 1992. Distribution and characteristics of hypoxia on the Louisiana shelf in 1990 and 1991. p. 15-20. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, _____, AND _____. 1994a. Hypoxia conditions in bottom waters on the Louisiana-Texas shelf. Pages 50-54 *In* M. J. Dowgiallo (ed.), Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding, Special NOAA Report, National Oceanic and Atmospheric Administration, Coastal Ocean Office, Silver Spring, Maryland.

_____, W. J. WISEMAN JR., AND R. E. TURNER. 1994b. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone of Louisiana. Estuaries **17**: 850-861.

RENAUD, M. 1986. Hypoxia in Louisiana coastal waters during 1983: implications for fisheries. Fish. Bull. **84**: 19-26.

RIEBESELL, U. 1989. Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom. Mar. Ecol. Prog. Ser. **54**: 109-119.

_____. 1991. Particle aggregation during a diatom bloom. II. Biological aspects. Mar. Ecol. Prog. Ser. **69**: 281-291.

ROY, S., AND S. A. POULET. 1990. Laboratory study of the chemical composition of aging copepod fecal material. J. Exp. Mar. Biol. Ecol. **135**: 3-18.

SACKETT, W. M., W. R. ECKELMANN, M. L. BENDER, AND A. W. H. BE. 1965. Temperature dependence of carbon isotope composition in marine plankton and sediments. Science **148**: 235-237.

SHUMAN, F. R. 1978. The fate of phytoplankton chlorophyll in the euphotic zone--Washington coastal waters. Ph.D. Dissertation. Washington State University.

SILVER. M. W., AND K. W. BRULAND. 1981. Differential feeding and fecal pellet composition of salps and pteropods, and the possible origin of deep-water flora and olive green "cell". Mar. Biol. **62**: 263-273.

SKLAR, F. H., AND R. E. TURNER. 1981. Plankton production in Louisiana coastal zone as influenced by the Mississippi River. Contrib. Mar. Sci. **24**: 93-106.

SMALL, L. F., M. R. LANDRY, R. W. EPPLEY, AND A. F. CARLUCCI. 1989. Role of plankton in the carbon and nitrogen budgets of Santa Monica Basin, California. Mar. Ecol. Prog. Ser. **56**: 57-74.

SMAYDA, T. J. 1969. Some measurements of sinking rates of fecal pellets. Limnol. Oceanogr. **14**: 621-625.

SMETACEK, V. S. 1980. Zooplankton standing stock, copepod fecal pellets and particulate detritus in Kiel Bight. Estuar. Coastal Mar. Sci. **11**: 470-490.

_____. 1985. Role of sinking in diatom life history cycles : ecological, evolutionary and geological significance. Mar. Biol. **84**: 239-251.

THAYER, G. W., J. J. GOVONI, AND D. W. CONNALLY. 1983. Stable carbon isotope ratios of planktonic food web in the northern Gulf of Mexico. Bull. Mar. Sci. **33**: 247-256.

TURNER, J. T. 1979. Microbial attachment to copepod fecal pellets and its possible ecological significance. Trans. Am. Microb. Soc. **98**: 131-135.

TURNER, R. E., AND R. A. ALLEN. 1982. Plankton respiration in the bottom waters of the Mississippi River Delta Bight. Contrib. Mar. Sci. **25**: 173-179.

_____, AND N. N. RABALAIS. 1991. Changes in Mississippi River water quality this century and implications for coastal food webs. BioScience **41**: 140-147.

_____, AND _____. 1994. Coastal eutrophication near the Mississippi river delta. Nature **368**: 619-621.

URBAN, J. L., C. H. MCKENZIE, AND D. DEIBEL. 1992. Seasonal differences in the content of *Oikipleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets: illustrations of zooplankton food web shifts in coastal Newfoundland waters. Mar. Ecol. Prog. Ser. **84**: 255-264.

URRERE, M. A., AND G. A. KNAUER. 1981. Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. J. Plank. Res. **3**: 369-387.

VOSS, M. 1991. Content of copepod faecal pellets in relation to food supply in Kiel Bight and its effect on sedimentation rate. Mar. Ecol. Prog. Ser. **75**: 217-225.

WASSMANN, P. 1983. Sedimentation of organic and inorganic particulate material in Lindaspollene, a stratified, land-locked fjord in western Norway. Mar. Ecol. Prog. Ser. **13**: 237-248.

WIEBE, P. H., S. H. BOYD, AND C. WINGET. 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Toungue of the Ocean, Bahamas, with a description of a new sedimentation trap. J. Mar. Res. **34**: 341-354.

CHAPTER 2

TEMPORAL VARIATION IN ZOOPLANKTON FECAL PELLET CARBON FLUX ON A RIVERINE-INFLUENCED INNER CONTINENTAL SHELF

INTRODUCTION

Large biogenically produced particles are primarily responsible for the transport of organic material from oceanic surface layers to the sea floor (Bishop et al. 1980, Honjo 1980, 1982, Shanks & Trent 1980, Knauer & Martin 1981, Silver & Alldredge 1981, Martin & Knauer 1982). These particles may include fecal pellets, fecal material, or strings of fecal pellets aggregated within marine snow. Copepod fecal pellets have received greater attention as the major mechanism for transport of particulate organic carbon to deeper waters (Lohmann 1902, Scharader 1971, Turner & Ferrante 1979, Dunbar & Berger 1981, Urrere & Knauer 1981, Fowler et al. 1983), because copepods form a large component of the zooplankton community, and their vertical migration has been reported to affect transport of material to deeper waters (Honjo & Roman 1978, Urrere & Knauer 1981, Sasaki et al. 1988). The importance of larvaceans, both their abundance and grazing potential, is receiving increasing attention, especially for coastal waters (Dagg & Ortner 1992).

Sinking rates of mesozooplankton fecal pellets are typically on the order of 10^1 to 10^3 m d^{-1} (Bienfang 1980, Madin 1982, Laws et al. 1988, Dilling & Alldredge 1993) compared to sinking rates of phytoplankton cells which sink 1 to 10^1 m d^{-1} (Smayda 1969, Bienfang 1980, Laws et al. 1988). Phytoplankton and small fecal pellets are more likely than larger particles to be consumed or remineralized in the water column. Rapidly sinking fecal pellets facilitate the transport of material out of the euphotic zone, including organic carbon, inorganic sediment, organic pollutants (Elder & Fowler 1977, Prahl & Carpenter 1979), trace elements, metals (Fowler et al. 1977), and radionuclides,

which make these particles (fecal pellets) potentially more important in marine biogeochemical cycles than other particles.

The percent contribution of carbon flux via zooplankton fecal pellets has been reported from many studies using sediment traps in the open ocean (Wiebe et al. 1976, Bishop et al. 1977, Honjo 1977, 1980, Knauer & Martin 1981, Urrere & Knauer 1981, Pilskaln & Honjo 1987, Deuser et al. 1981) and in shallow and coastal areas (Smetacek 1980, Dunbar & Berger 1981, Shuman 1978, Bochdansky & Herndl 1992, Fukuchi et al. 1993). These studies show that the fecal pellet contribution (by weight) to the vertical carbon flux varies from 1% (Pilskaln & Honjo 1987) to more than 90% (Bathmann et al. 1987) and is a function of seasonal surface production, zooplankton grazing activity, nutrients and depth. It has also been estimated that zooplankton fecal pellets can provide up to 66% of the benthic community carbon requirement (Pilskaln & Honjo 1987).

The importance of fecal pellets in the sedimentation of organic material depends largely on their sinking rates and their degradation. The sinking rate of fecal pellets depends on their size and density (Deibel 1990, Urban et al. 1992). The density of fecal pellets depends upon the quality of food ingested (Bienfang 1980, Dagg & Walser 1986, Voss 1991, Urban et al. 1992). Fecal pellet degradation increases the residence time of fecal pellets in upper water layers and, therefore, retards the vertical flux (Peinert et al. 1989, Paffenhofer & Knowles 1979, Lampitt et al. 1990, Noji 1991). Degradation is promoted via various mechanisms including coprophagy (reingestion of fecal pellets by zooplankton), coprorhexy (mechanical breakage of fecal pellets by organisms), and coprochally (loosening of fecal pellets). Degradation of particulate carbon and the peritrophic membrane of fecal pellets is enhanced at temperatures $> 15\ ^{\circ}C$ (Honjo & Roman 1978, Roy & Poulet 1990).

The carbon flux of sedimenting fecal pellets can also be affected by rapid diffusion (hours to days) of fecal pellet carbon to the dissolved organic carbon (DOC)

pool (Jumars et al. 1989). The loss to the DOC pool can be as great as 90%, and this DOC may fuel bacterial production that further promotes pelagic microbial recycling of material in the water column (Jumars et al. 1989). Thus, regional and seasonal differences in the relative contribution of fecal pellets to carbon flux result from differences in their content or biological modification.

The export of carbon from surface waters to the lower water column and sediments is particularly interesting on the southeastern Louisiana shelf where the oxidation of fluxed organic material from surface layers leads to oxygen deficiency in the bottom waters. The continental shelf adjacent to the outflows of the Mississippi-Atchafalaya River system is an extremely productive coastal system. Primary production near the Mississippi River delta averages 329 g C m^{-2} yr^{-1} in the plume region (Lohrenz et al. 1990) and 290 g C m^{-2} yr^{-1} on the southeastern shelf (Sklar & Turner 1981). Variation in primary production and chlorophyll biomass in the plume is explained by changes in light characteristics, salinity, temperature, mixed layer depth and nutrient availability (Lohrenz et al. 1990, 1994, Sklar & Turner 1981). Changes in nutrient concentrations, loadings and ratios in the effluents of Mississippi and Atchafalaya rivers have occurred since the mid-1950s with doublings of nitrate and total phosphorus and a reduction of 50% in silicate (Turner & Rabalais 1991, 1994). Shifts in stoichiometric nutrient balance in the Mississippi River plume with increased potential for silica limitation relative to nitrogen and phosphorus limitation (Justic' et al. in press a, b, Turner & Rabalais 1991, 1994, Dortch & Whitledge 1992) suggest a scenario for increased productivity, as well as a shift in the composition of phytoplankton communities and higher trophic levels (e.g. zooplankton communities). These complex interactions may ultimately affect the overall trophic structure, regeneration of nutrients, remineralization of carbon, and the fate of carbon on the continental shelf. Quantification of the fecal pellet fluxes on this shelf and their role in carbon fluxed to the sea foor were non-existent prior to this study.

The incidence of oxygen-depleted bottom waters in coastal areas is increasing worldwide and is apparently related to eutrophication (Turner & Rabalais 1994, Rabalais et al. 1991). The bottom water hypoxic zone (< 2 mg O_2 l^{-1}) in the northern Gulf of Mexico covers up to 16,500 km^2 on the inner continental shelf, from the Mississippi River delta to the upper Texas shelf, and is the largest among such areas in the Western Atlantic Ocean (Rabalais et al. 1991, 1994a). Hypoxic bottom waters occur primarily from April to October and form large, persistent and severe zones from June through August. The temporal variation in the distribution of hypoxia is related to timing and magnitude of Mississippi River discharge, large-scale circulation patterns, solar heating and wind events. The formation of hypoxic bottom water in this system depends on strong density stratification, high inputs of organic matter, and respiration rates sufficient to deplete bottom water oxygen concentrations faster than resupply (Rabalais et al. 1991, 1992). The carbon flux to bottom waters, when metabolized, directly influences the oxygen concentration of bottom layers and, indirectly, benthic and pelagic species distributions and element cycling.

Many factors affect the flux of the surface organic production to the seabed on the southeastern Louisiana continental shelf. Large-scale circulation patterns may advect surficial plume waters to great distances from the immediate river delta. Primary productivity can be recycled within the upper mixed layer by zooplankton grazing or bacterial remineralization. The importance of bacterial remineralization is demonstrated by high water column respiration rates and high bottom water respiration rates (Turner & Allen 1982, Chin-Leo & Benner 1992, Dortch et al. 1994). Positive correlations between community respiration and chlorophyll concentration indicate phytoplankton as the source of organic carbon being respired (Turner & Allen 1982). Carbon fixed by primary productivity is either sedimented directly as phytoplankton biomass (Smetacek 1980, Wassmann 1983, Dortch et al. 1992) or is integrated into larger particles by production of fecal pellets (Angel 1984, Dunbar & Berger 1981,

Wiebe et al. 1976, Honjo 1977, 1980, Honjo & Roman 1978, Pilskaln & Honjo 1987, Small et al. 1983, 1989) and/or aggregate formation (Alldredge & Gotschalk 1989, 1990, Riebesell 1989).

Surface water net production (oxygen surplus) measured on the southeastern Louisiana shelf (station C6B of this study) lags one month after peak river flow and bottom oxygen deficiency lags two months after peak river flow (Justic' et al. 1993). Strong cross correlations between these factors implicates riverine delivery of nutrients rather than regeneration as the source of nutrients supporting net production and subsequent oxygen deficiency. Justic' et al. (in preparation) modeled oxygen fluxes for a station on the southeastern Louisiana shelf (station C6B of this study) and demonstrated that net production in surface waters integrated over the period from February to June (92 g C m^{-2} d^{-1}), if fluxed as particulate carbon to the lower water column and seabed, is sufficient to produce and maintain hypoxia without further additions. The likely mechanism for carbon to reach the bottom is sinking particles, including fecal pellets, phytoplankton cells and aggregates.

The time lags between peak river flow and net surface production and bottom oxygen deficiency further implicate changes in riverine nutrient delivery with changes in trophic structure. During spring peak river flow, sufficient nutrients are available in an appropriate ratio to support phytoplankton production without silica limitation. Grazing is unlikely to reduce the high phytoplankton biomass (M. J. Dagg pers. comm.), and phytoplankton cells are more likely to settle than compared to the summer (more silica, less loss of primary production by grazing). Later, in late spring and early summer, when silica concentrations are lower (fewer diatoms) and a more mature zooplankton community exerts greater control on phytoplankton biomass by grazing, fecal pellet flux is likely to surpass direct cell sinking in relative carbon flux. Also fecal pellets, being larger in size, are more likely to sink than phytoplankton cells. The likelihood of this seasonal progression in the relative contribution of phytoplankton

versus fecal pellet flux is supported by a study which demonstrated a similar gradient of diatom flux with distance from the river delta and decrease in silicate availability (Dortch et al. 1992).

The seasonal varability in nutrient loading and nutrient ratios, water column stability, temperature and phytoplankton community composition are thus all potentially important factors driving variations in the quality and quantity of organic loading to bottom waters on this shelf. Knowledge of the fecal pellet fluxes from surface to bottom waters may reveal important aspects of the present continental shelf trophic structure. The purpose of this study was to estimate the temporal variations in fecal pellet flux on this shelf to both quantify its contribution to the surface to bottom water carbon flux and to thereby learn more about the trophic structure of the continental shelf.

OBJECTIVES

The objective of this study was to determine the temporal variability of fecal pellet flux to the lower water column and sediments on a continental shelf influenced by the Mississippi River effluent and also subject to seasonally severe hypoxia. I determined differences in fecal pellet vertical fluxes over a two-year period at two depths in the water column. I made conversions of fecal pellet volumes and numbers to carbon equivalents to estimate the temporal variability in fecal pellet carbon flux within the water column and by pellet size. I tested the following hypotheses:

- fecal pellet flux is greater in the summer when zooplankton communities are more mature, and
- the larger pellets dominate the fecal pellet flux.

Differences in the relative contribution of micro- and mesozooplankton, as well as differences related to depth in the water column and season, were determined and

placed within the context of the environmental variability of the system. Ultimately, the relative importance of fecal pellet carbon flux to the total carbon export from the surface waters and its potential to support oxygen deficiency in bottom waters were determined (Chapter 3).

METHODS

Instrument Mooring

Sediment traps on a permanent mooring were deployed at a station, C6B, in 20 m water depth, located at 28°50.41' N and 90°26.03' W off Terrebonne Bay on the southeastern Louisiana coast (Fig. 1.1). The station is in the center of the area where hypoxic bottom water conditions prevail during summer (Rabalais et al. 1991, 1992, 1994b). The mooring was deployed from April 17 through December 7, 1991 and from March 2 through October 27, 1992.

The mooring was weighted with an anchor and buoyed with a subsurface float. The mooring was attached to a nearby (~40 m distant) platform by a heavy chain. One of the sediment traps was attached to the mooring cable at 5 to 6 m, within the upper mixed layer (designated "top"), and the other at 15 m, below the usual pycnocline (~ 10 m), and within the lower water column where hypoxia develops most summers (designated "bottom"). A current meter was located near each trap, and an oxygen meter was attached to the cable 1 m above the bottom (19 m). A light meter was attached periodically to the mooring at 9 m depth (Fig. 1.3).

The sediment trap consisted of a simple cylinder with a surface area of 0.45 m^2 and an aspect ratio of 3:1 (Prior et al. 1987). The cylinder narrowed into a funnel at the lower end. Sediments and particles were collected in acrylic tubing (0.5 m long, 4.5 cm diameter) at the base of the funnel. The surface opening of the trap was baffled to reduce turbulence over the trap opening. A brine solution (~ 45 ppt) was added to the

collection tubes to prevent back flushing. Glutaraldehyde (2% final volume) was added as a preservative. Sediment trap servicing and sample collections occurred at one or three week intervals in 1991 as weather permitted. Sampling in 1992 was usually every two weeks, again depending on weather. Samples were kept cool and returned immediately to the laboratory for processing.

Surficial Sediment Collections

Three replicate sediment samples were collected at monthly intervals from the study site, either by divers using syringe corers near the base of the mooring, or with a box core (500 m from the mooring) subsampled with syringe corers. All sediment cores were refrigerated until processing (< 24 h). In the laboratory, water was carefully siphoned leaving 1 cm of overlying water which was carefully retrieved, without disturbing the sediment surface, and placed in a scintillation vial. The top 2 mm of sediment was precision extruded, sliced from the core and added to the same scintillation vial. Glutaraldehyde (2 ml of 50%) was added, and the sample volume was increased to 20 ml with filtered sea water. Samples were refrigerated until analysis.

Ancillary Measurements

Ancillary hydrographic data, including temperature, salinity, density and dissolved oxygen, were recorded with a Hydrolab Surveyor 3 or SeaBird CTD unit during each servicing of the sediment traps and at several additional times during the study. Biological data included water column pigments (chlorophyll *a* and phaeopigments) and nutrients collected at the surface, above (6.5 m) and below the pycnocline (14 m), and at the bottom (~ 19 m). Depths of mid-water collections corresponded to the depths of the openings of the sediment traps.

Additional sediment samples were collected from the box core or by divers for analysis of pigments (chlorophyll *a* and phaeopigments), total organic carbon, and

sediment grain size (Robertson et al. 1980, Rabalais et al. 1992, Rabalais et al. 1993, Turner & Rabalais 1994).

Fecal Pellet Enumeration and Flux Calculations

Each sample (trap or surficial sediments) was split in a Folsom plankton splitter to dilute the fecal pellets to a countable density. The last split of material was stained with proflavine and filtered through nested screens of 63 and 20 µm Nitex screen. The particulate matter retained on the screens was backwashed onto an 8 µm cellulose (Millipore) filter, which was then mounted on a glass slide and cleared with immersion oil. Fecal pellets were counted under epifluorescence and the length and width were measured. Fecal pellet volume (FP vol μm^3 $pellet^{-1}$) was calculated for each fecal pellet by using a formula for prolate spheroids (Q. Dortch pers. comm.):

$$\text{FP vol } (\mu m^3 \text{ pellet}^{-1}) = 0.523 * C^3 * L * W^2 \qquad \text{Equation 2.1}$$

where C is the conversion factor depending on magnification (µm $division^{-1}$), L is the length and W is the width of the fecal pellet (in divisions). A mean fecal pellet volume was determined for each sample and size fraction.

The total number of fecal pellets in each trap and the surficial sediments was calculated using the following formulae:

$$\#\text{ FP split}^{-1} = (\#\text{ FP counted}/\ \#\text{ parts of filter counted}) * (\#\text{ parts filter}^{-1}) \qquad \text{Equation 2.2}$$

where # parts of filter counted was equal to # of strips counted, 0.5 for half of the filter counted and one for the whole filter counted. The # parts $filter^{-1}$ was equal to one for the whole filter, two for the half filter and a factor of 10.84 and 21.7 at 10x and 20x magnification, respectively, for the each strip counted (Q. Dortch pers. comm.).

$$\#\ FP\ sample^{-1} = \#\ FP\ split^{-1} * 2^{(n-1)} \qquad \text{Equation 2.3}$$

where n is the number of splits.

The fecal pellet flux (FP flux) into the sediment trap was calculated as follows:

$$FP\ Flux\ (no.\ m^{-2}\ d^{-1}) = (\#\ FP\ sample^{-1})/(area\ of\ trap\ mouth * duration\ of\ deployment) \qquad \text{Equation 2.4}$$

Fecal pellet flux could not be calculated for surficial sediments because accumulation rates were not known. Fecal pellet abundance (no. m^{-2}) was calculated as follows:

$$FP\ density\ (no.\ m^{-2}) = (\#\ FP\ sample^{-1})/surface\ area\ of\ collector \qquad \text{Equation 2.5}$$

Estimation of Fecal Pellet Carbon

Fecal pellet carbon flux into the traps and fecal pellet carbon in the sediments were calculated from the data on average fecal pellet volume (for all sizes and shapes of fecal pellets and for each size fraction). A volume to carbon ratio was determined for copepod fecal pellets collected in the laboratory that compared well with values reported in the literature (Table 2.1). Values of Strathmann (1967), Mullin et al. (1966), and Elder (1979), which were based on a volume to carbon ratio for phytoplankton, were used most frequently. Another relationship, based on 20% C in dry weight (per fecal pellet of shrimp *Palaemonetes pugio*) (Johannes & Satomi 1966),

Table 2.1. Comparison of fecal pellet (FP) carbon to volume ratios for different organisms.

Organisms	FP Carbon (μg C pellet^{-1})	FP Carbon: volume (μg C μm^{-3})	Reference
Salps		0.77-4.67*10^{-8}	Madin 1982
Copepods	0.142	5.66*10^{-7}	Honjo & Roman 1978
Copepods	0.154	4.27*10^{-7}	Abou Debs 1984
Salps	0.107	0.77 - 4.67*10^{-7}	Bochdansky & Herndl 1992
Copepods		2.25*10^{-7}	Urban 1992
Chaetognaths		0.77-2.77*10^{-8}	Dilling & Alldredge 1993
Copepods	*0.202*	*8.35*10^{-7}*	*This study*

is often used to calculate fecal pellet carbon. Other laboratory estimates of direct fecal pellet carbon measurements are given in Table 2.1.

Freshly collected copepods were used to estimate fecal pellet carbon to volume ratios. A surface plankton tow with a standard plankton net (0.5 m mouth diameter and 224 μm mesh) was taken near station C6B at intermediate salinities (20-22 ppt). The cod end was emptied into a 20 l carboy filled with water from the collection site. Samples were immediately brought back to the laboratory. Copepods, usually *Acartia tonsa,* were sorted (within 20 to 30 minutes) from the sample. Copepods (50 to 100) were added to five culture bowls with 250 ml filtered (20 μm) ambient sea water from the collection site. Copepods were removed after two hours by filtering through a 153 μm Nitex screen. Fecal pellets were concentrated by filtering through 20 μm Nitex screen and back washed into a petri dish. The petri dish was kept on ice to decrease metabolic activity and possible DOC loss. Three replicate samples of 50, 100 and 150 fecal pellets were picked within 10 to 20 minutes and filtered through precombusted (360 °C, 5 h) GF/F filters. Each experiment was repeated three times. Filters were dried at 50 °C and analyzed for carbon and nitrogen on a Control Equipment Elemental Analyzer, model 240XA, with a multi-sample injector. A sample of 50 fecal pellets was picked for length and width measurements to calculate volume of the fecal pellets.

Fecal pellet carbon to volume ratio was estimated by calculating the average fecal pellet carbon (μg C $pellet^{-1}$) and relating it to the average fecal pellet volume (μm^3). The estimate obtained was very close to values in the literature (Table 2.1) and was used to estimate fecal pellet carbon in sediment traps and surficial sediments.

Statistical Analyses

A repeated measures analysis is desirable when fixed stations are sampled through time (Maceina et al. 1994). A univariate split-split plot design, where class variables are assigned to subunits, was used to analyze the variability in fecal pellet

data. A greater amount of information can be obtained when class variables are assigned to subunits (Steel & Torrie 1980). The split-split plot design was also appropriate to use in this case because samples were collected at a fixed station over time and, therefore, violated the assumption of random sampling required for parametric procedures such as analysis of variance (ANOVA). A fixed station may display features unique and specific to a location with temporal variations, and any correlation between the treatments also violates an assumption of ANOVA. A repeated measures ANOVA or a split plot design has been employed for ecological experiments where data were repeatedly collected from the same organism and for fisheries data collected at fixed stations over time (Maceina et al. 1994). This technique partitions the variation due to fixed sampling site, treatments or manipulations, correlation that may occur over time, and interactions among class variables (year, season, depth and size fraction). Partitioning increases accuracy and provides new insights on different responses of the variables.

The split-split plot design was divided into a main plot which included year, season and year*season interaction. Replication was sought from different dates by partitioning sample dates into the seasons, spring, summer and fall (Appendix B). This division was based on hydrography and vertical structure of the water column rather than the calendar year. The summer period was distinguished from spring and fall by having a relatively stable water column, a strong pycnocline (around 8 to 15 m) (Figs. 2.1 & 2.4) that separated a low dissolved oxygen bottom layer from oxygen saturated surface waters, and negligible bottom water currents (2-3 cm s^{-1}) (W. J. Wiseman, Jr. unpubl. data).

Depth (5-6 m = top trap, 15 m = bottom trap) and interactions between depth*year, depth*season, and depth*year*season were in the first subplot-A. The two size fractions (> 63 μm, > 20 μm) and their interactions with other treatments were examined in the second subplot-B to identify significant differences in the contribution

of different sized fecal pellets (potentially originating from meso- or micro-zooplankton) to the flux. Tukey's studentized range test, a pair-wise comparison, was employed to specify inter-annual, seasonal, and depth related variability, because it is more conservative than other tests and has a family-wise error rate.

The assumptions for normally distributed data and homogeneity of variance were tested by univariate analysis and plotting residuals. When data were not normally distributed (Shapiro-Wilk statistics, $Pr < W = 0.0001$) and the mean values were proportional to their variances, data were transformed to $\log_{10}$ values to stabilize variances for the analyses. Because of the unbalanced data, Type III sum of squares were used to compute mean square errors (Steel & Torrie 1980).

Fecal pellet flux and fecal pellet carbon flux data were correlated with environmental data including water temperature and salinity, total pigments, delta sigma t (density difference between surface and bottom, a measure of the strength of the pycnocline) and surface water salinity lagged one month. The upper water column (U) was an average of surface water and 6.5 m depth, and the lower water column (L) was an average for 14 m depth and bottom. A best fit model was developed from the environmental variables using a stepwise multiple regression model with foreward selection.

All statistical analyses were done on PC SAS version 6.04 (SAS Institute 1985).

Resuspension Potential of Fecal Pellets

I examined the potential of bottom currents to resuspend fecal pellets by determining the critical bed shear stress from Shield's entrainment function, applying nominal diameters for the volume of fecal pellets and assuming a constant density of fecal pellets (Appendix A). I calculated critical velocity (U*) at 1 m above the seabed. A limited current meter record from 1 m above the bed (Endeco model 174) was obtained for May 10 to August 24, 1992 (W. J. Wiseman, Jr. unpubl. data). Other

records from the bottom current meter in 1991 and 1992 deployments were not reliable (W. J. Wiseman, Jr. pers. comm.).

RESULTS

Characteristics of the Water Column

A stratified system dominated most of both years. The density distribution was controlled primarily by salinity (Figs. 2.1 and 2.2). The water column was mostly isothermal in spring and fall of both years; however, solar heating of the upper water column contributed to the development of a thermocline and an increased density gradient in summer. Dissolved oxygen concentrations were low (< 2 mg O_2 l^{-1}) from June through the end of August (days 177-237) in 1991 and from late May through late August (days 149-237) in 1992 (Figs. 2.1-2.4). The periods of hypoxia coincided with greater surface-to-bottom differences in density. The stable, stratified water column was disrupted by a series of frontal passages in fall 1991 and the passage of Hurricane Andrew on August 25, 1992 and subsequent cold fronts. The water column remained well mixed through the fall of 1991, but a stratified system reestablished in fall of 1992.

Nitrate concentrations were high in surface waters in spring of both years (Figs. 2.5 and 2.6). High nitrate concentrations were also evident in bottom waters in spring and occasionally in summer. The concentrations of silicate, phosphate and ammonia were elevated in surface waters in spring 1991, but were not as high in 1992. Nitrite concentrations were higher in bottom waters in summer of both years, with small peaks in surface as well as bottom waters in fall. Bottom water silicate, phosphate and ammonia concentrations were usually higher in summer in both years.

Chlorophyll *a* concentrations were high in surface waters in late spring (April-May) of both years (Figs. 2.7 and 2.8). Very high chlorophyll *a* concentrations were seen in bottom waters in summer 1992. Chlorophyll *a* concentrations were more

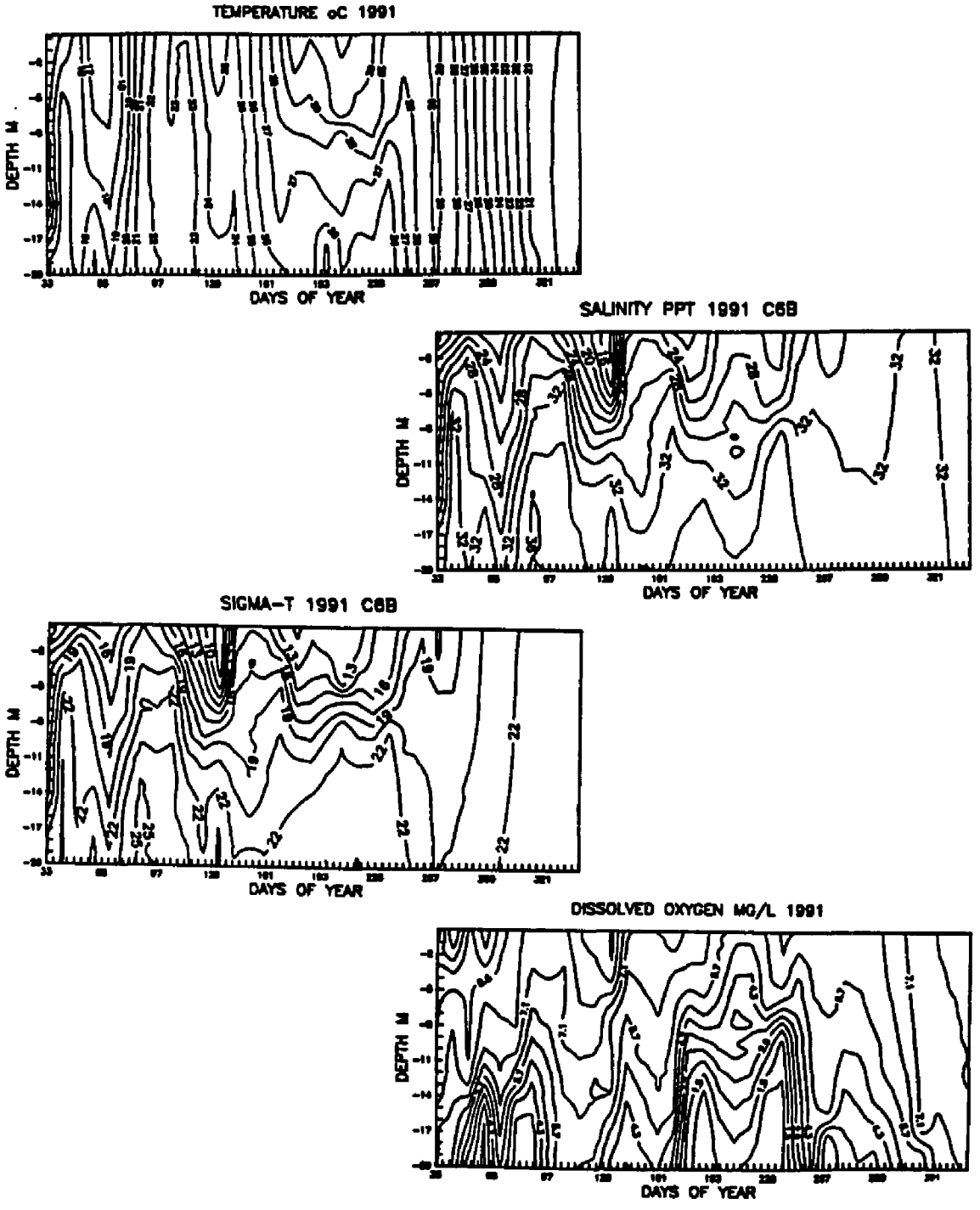


Figure 2.1. Hydrographic data collected during 1991 at station C6B; temperature (^{o}C), salinity (ppt), density (sigma-t) and dissolved oxygen (mg l^{-1}).

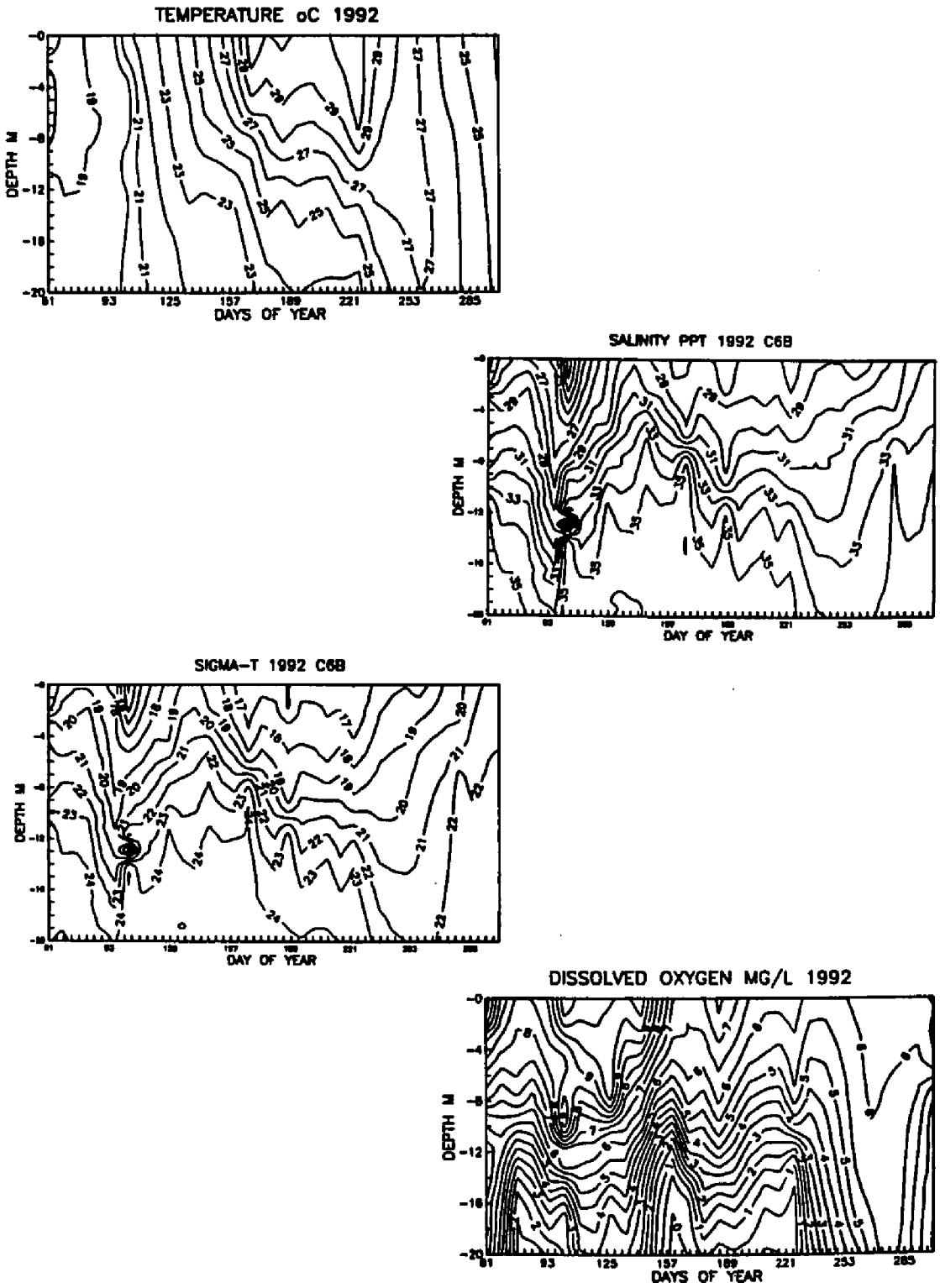


Figure 2.2. Hydrographic data collected during 1992 at station C6B; temperature (^{o}C), salinity (ppt), density (sigma-t) and dissolved oxygen (mg l^{-1}).

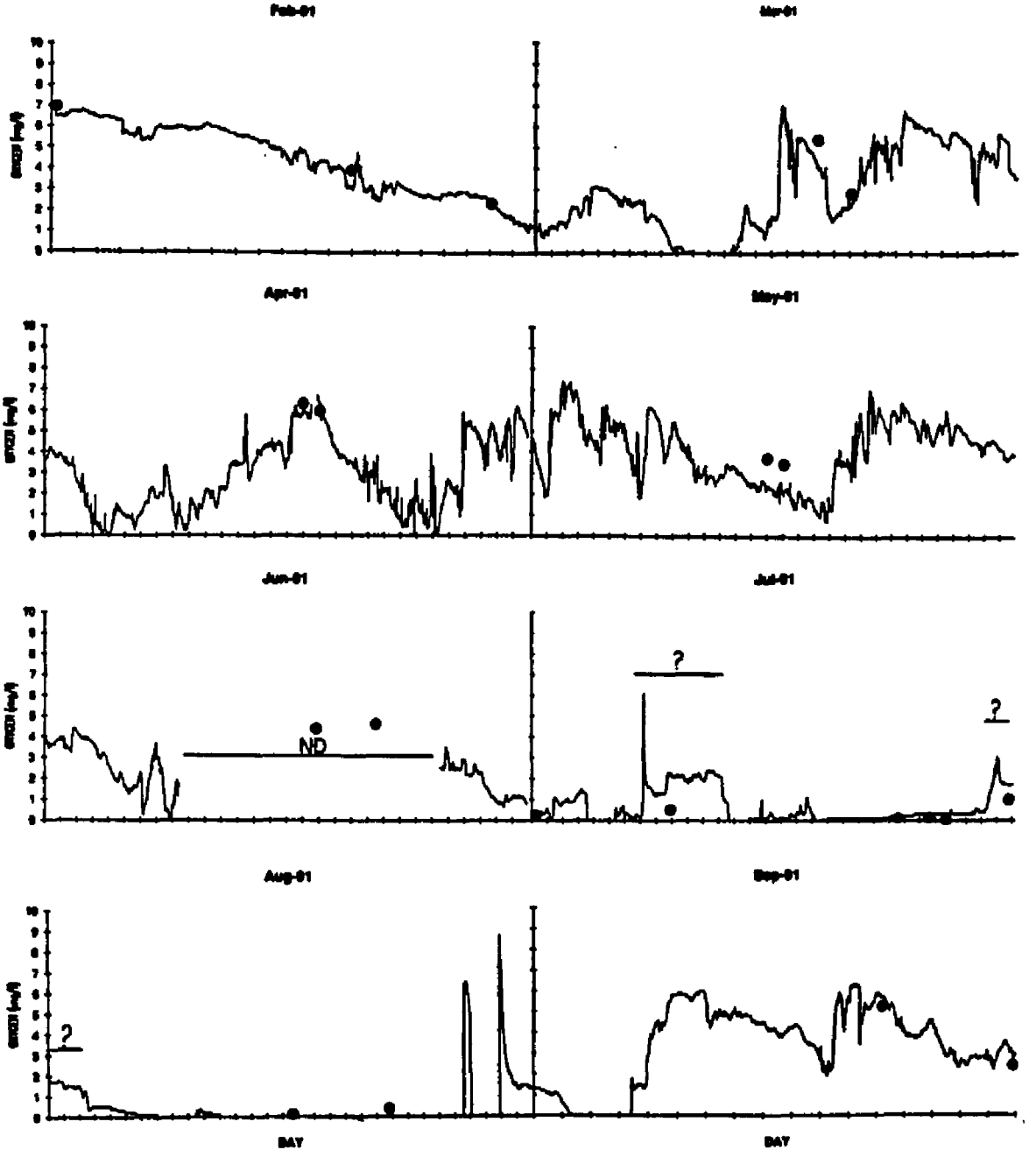


Figure 2.3. Time series of bottom water dissolved oxygen (mg l^{-1}) from the moored oxygen meter (19.5 m) at station C6B in 1991, solid circles are Hydrolab data obtained during C transect cruises, ? are suspicious data, and ND are no data.

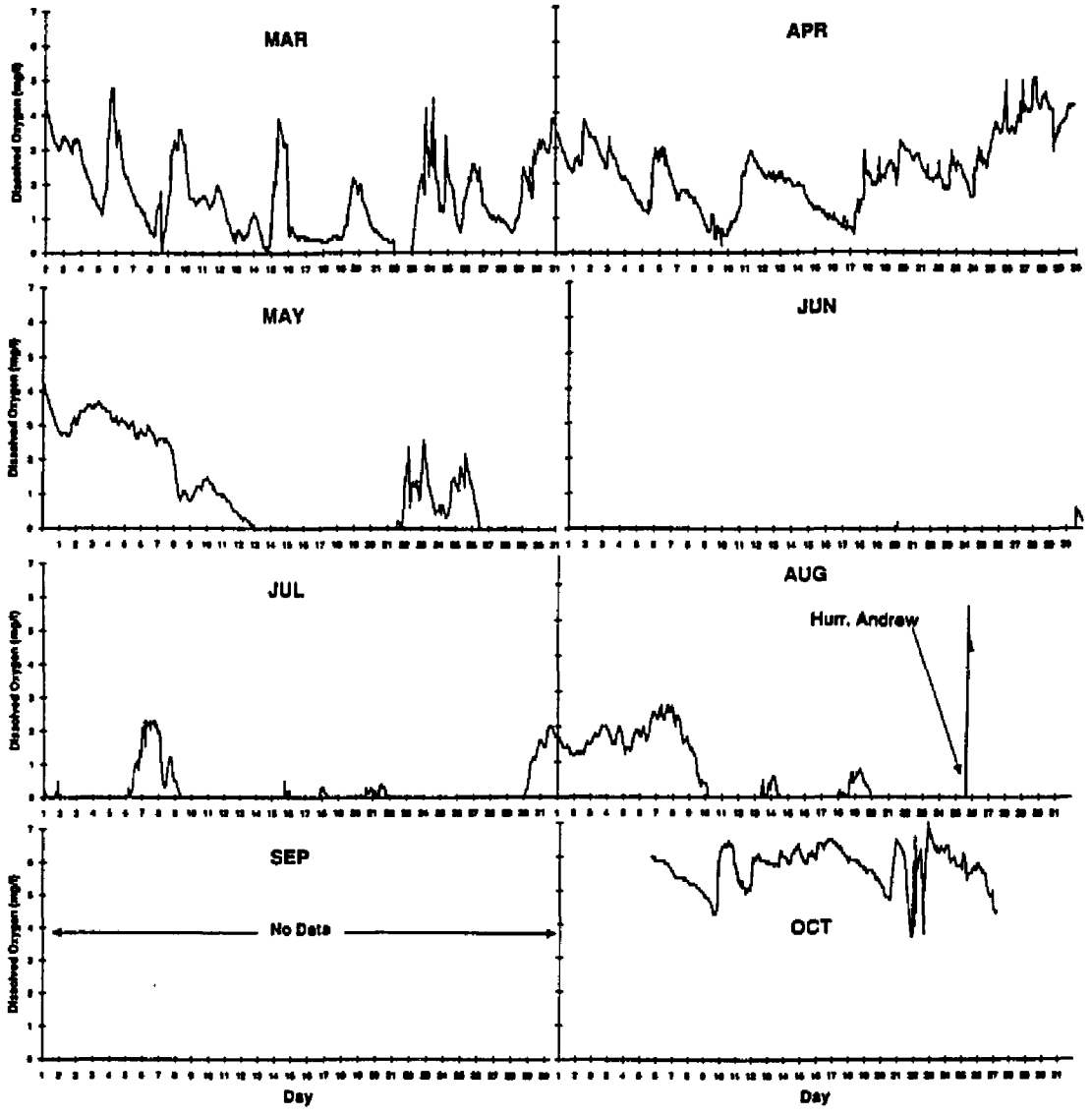


Figure 2.4. Time series of bottom water dissolved oxygen (mg l^{-1}) from the moored oxygen meter (19.5 m) at station C6B in 1992.

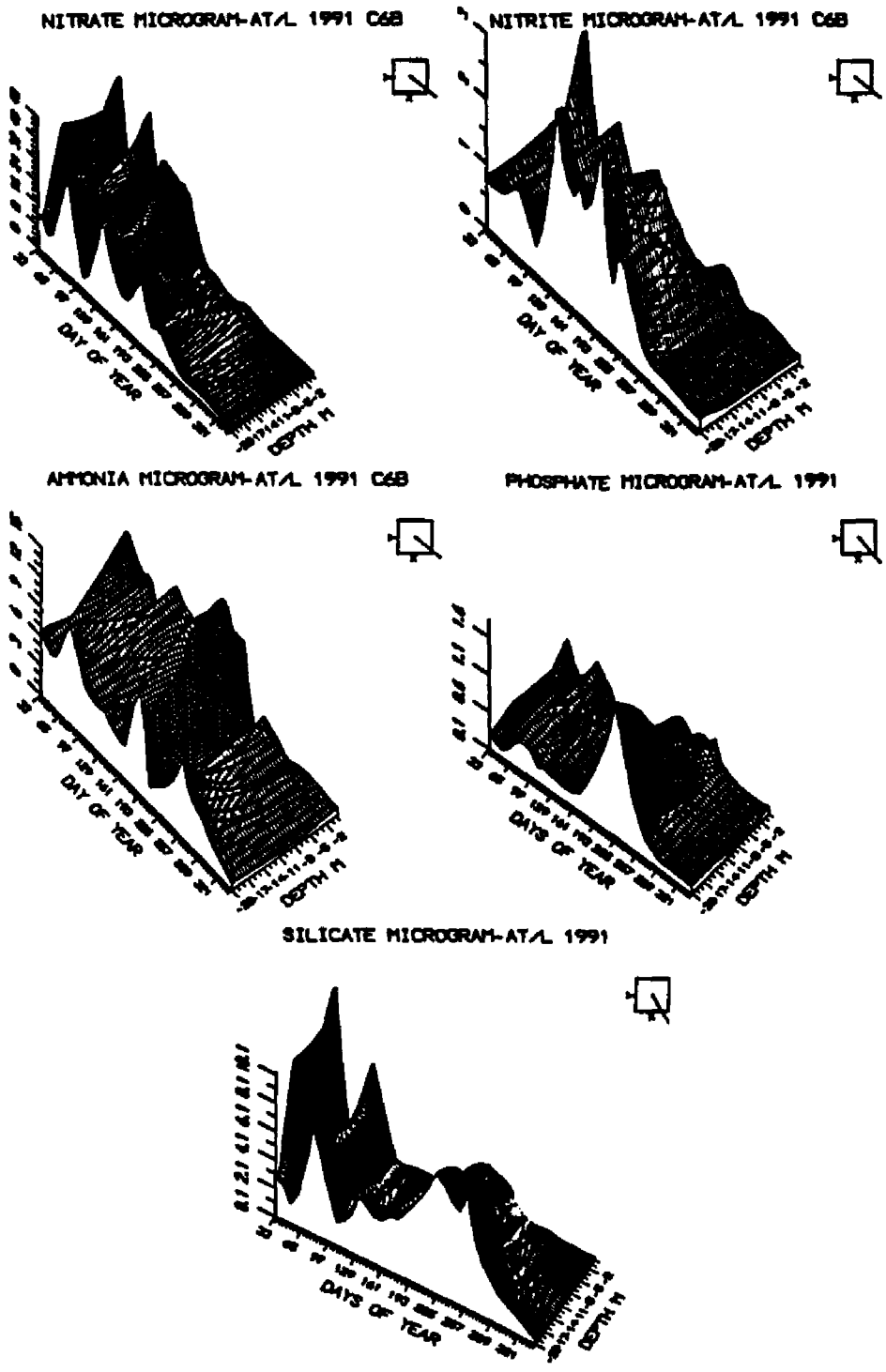


Figure 2.5. Nutrient concentrations in the water column at station C6B in 1991; nitrate (μg-at l^{-1}), nitrite (μg-at l^{-1}), ammonia (μg-at l^{-1}), phosphate (μg-at l^{-1}) and silicate (μg-at l^{-1}).

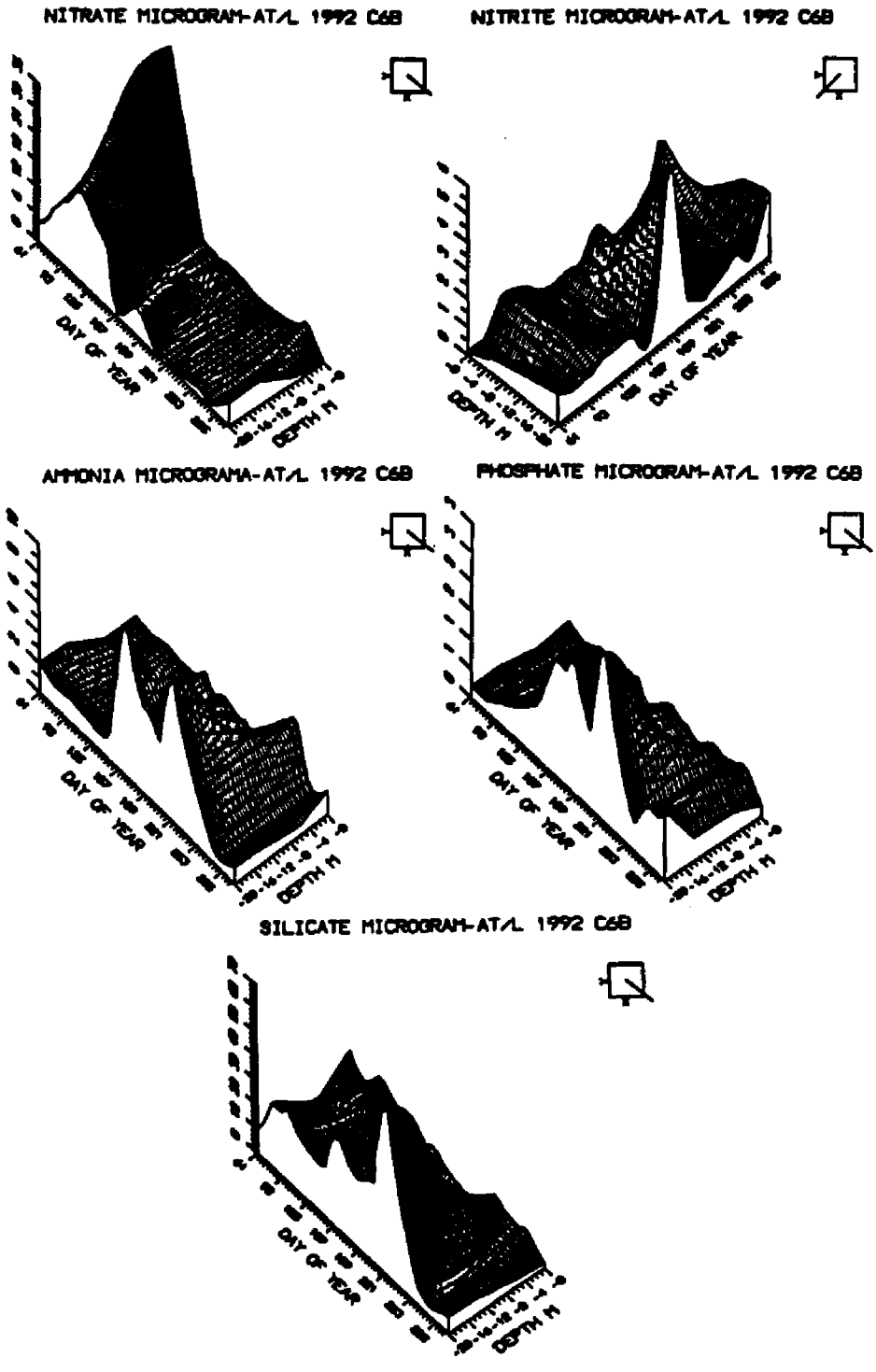


Figure 2.6. Nutrient concentrations in the water column at station C6B in 1992; nitrate (μg-at l^{-1}), nitrite (μg-at l^{-1}), ammonia (μg-at l^{-1}), phosphate (μg-at l^{-1}) and silicate (μg-at l^{-1}).

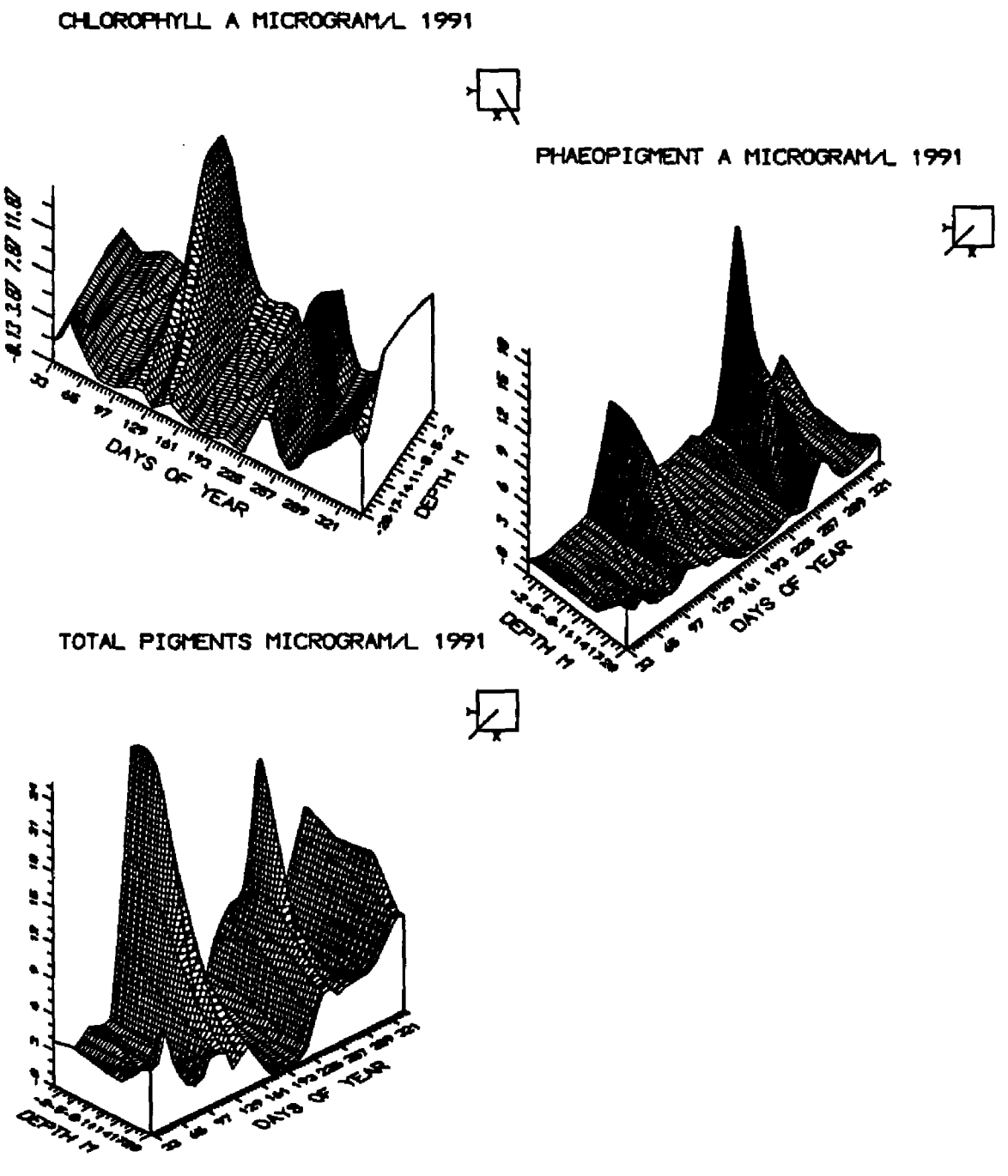


Figure 2.7. Pigment concentration in the water column at station C6B in 1991; chlorophyll *a* (µg l^{-1}), phaeopigments (µg l^{-1}), and total pigments (µg l^{-1}).

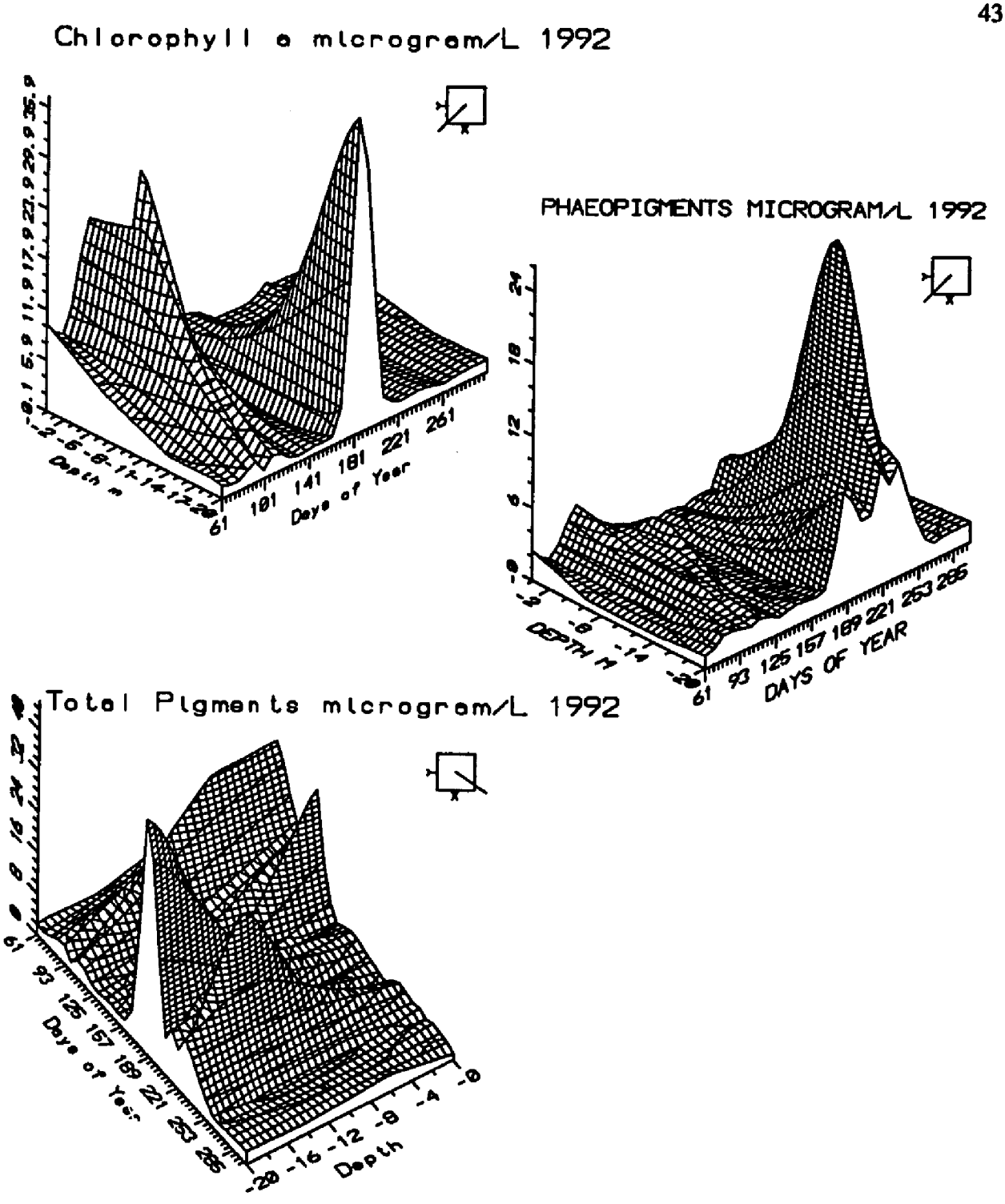


Figure 2.8. Pigment concentration in the water column at station C6B in 1992; chlorophyll *a* (µg l^{-1}), phaeopigments (µg l^{-1}), and total pigments (µg l^{-1}).

moderate throughout the water column in summer and fall of 1991. Phaeopigment concentrations were high in the upper water column in spring and fall of 1991 and fall 1992, and high in bottom waters of summer 1992.

Characteristics of Fecal Pellets

Sediment trap materials included phytoplankton, molts and appendages of zooplankton, intact and broken fecal pellets, and amorphous material. Intact fecal pellets were enclosed in a peritrophic membrane, and their contents were hard to discern. Whole cells or frustules of diatoms, and amorphous lithogenic and detrital material, however, could be seen in broken fecal pellets. Three different forms of fecal pellets were distinguished: cylindrical, ellipsoidal and tubular. Cylindrical fecal pellets were present in low numbers in all trap samples and were usually very fragile. These cylindrical fecal pellets (length 70 - 285 μm) were likely produced by copepods but most likely remained in the upper water column, because copepod fecal pellets do not always sink out of the surface zone (Smetacek 1980, Bathmann & Liebezeit 1986, Bathmann et al. 1987). The ellipsoidal fecal pellets (length 60-250 μm) were most abundant and were found in both size fractions. This suggests that they are an important component of the fecal pellet carbon flux. These ellipsoidal pellets were possibly produced by smaller copepods and larvaceans (Sasaki & Nishizawa 1981, Miquel et al. 1994, M. J. Dagg pers. comm.). Copepods and larvaceans were dominant zooplankters in the vicinity of the sediment traps as identified from surface zooplankton tows (Chapter 4) and water column samples of meso- and microzooplankton (Chapter 5). The third type of fecal pellet was large (length 300-600 μm), tubular and usually had broken ends. These fecal pellets were possibly produced by macrozooplankton and usually contained diatoms and unidentifiable amorphous material, and, when present, significantly influenced the total fecal pellet carbon flux values.

Fecal Pellet Flux

The fecal pellet flux ranged on the order of 10^4 to 10^7 $m^{-2} d^{-1}$. The average fecal pellet flux for 1992 was an order of magnitude greater than for 1991, but the between-year difference was not significant (Tables 2.2 and 2.3), probably because of the large variance. Fecal pellet flux varied significantly between seasons. The flux was significantly higher in fall than in spring and summer (Tables 2.2 and 2.3). The flux of fecal pellets varied up to two orders of magnitude difference between depths, averaging one order of magnitude higher in the bottom trap across both years (Fig. 2.9, Appendix B); the depth differences were significant (Tables 2.2 and 2.3). The number of fluxed fecal pellets in the > 20 μm size fraction was greater than the number in the > 63 μm size fraction in all cases (Fig. 2.10); the size fraction differences were significant (Tables 2.2 and 2.3). The percentage of the sample composed of smaller fecal pellets (> 20 μm) compared to larger fecal pellets (> 63 μm) was higher in both the top and bottom traps in both years (Fig. 2.10), with a few exceptions in spring and summer of 1991.

Fecal Pellet Carbon Flux

The carbon flux as fecal pellets ranged from 1.5 to 4818 mg C $m^{-2} d^{-1}$ (Fig. 2.9, Appendix B). The average fecal pellet carbon flux in 1991 was one order of magnitude greater than the average for 1992, but the difference was not statistically significant (Tables 2.2 and 2.3). The seasonal differences in fecal pellet carbon flux were significant, but the means overlapped considerably with the flux in spring being much greater than in summer. The flux in fall was intermediate between them (Tables 2.2 and 2.3). The fecal pellet carbon flux was higher in the top trap than the bottom trap in 1991, which was largely due to the presence of larger, tubular fecal pellets in the top trap, especially in spring and summer. On the other hand, the average fecal pellet carbon flux was higher in the bottom trap than in the top trap in 1992, but this was not

Table 2.2. Split-split plot design ANOVA for fecal pellet flux (no./m^2/d) and fecal pellet carbon flux (mg C/m^2/d) collected at station C6B during 1991 and 1992.

Source	df	Fecal pellet† P > F	Fecal pellet carbon† P > F
Model	63	0.0001*	0.0001*
**Main plot			
Year	1	0.9211	0.4609
Season	2	0.0001*	0.0001*
Year*Season	2	0.0027*	0.0011*
Error-1	21	0.0001*	0.1093
***Sub-plot A			
Depth	1	0.0001*	0.0083*
Year*Depth	1	0.0142*	0.0073*
Season*Depth	2	0.3029	0.4924
Year*Season*Depth	2	0.1098	0.0205*
Error-2	19	0.0001*	0.1053
Sub-plot B			
Size Fraction (SF)	1	0.0001*	0.0001*
Year*SF	1	0.0001*	0.0003*
Season*SF	2	0.2017	0.0419*
Depth*SF	1	0.9711	0.0181*
Season*Depth*SF	2	0.4029	0.9671
Year*Season*SF	2	0.7096	0.7353
Year*Season*Depth*SF	3	0.3459	0.9628

* significant at alpha error = 0.05
** test of hypothesis used error-1 = Date(year*season)
*** test of hypothesis used error-2 = Date(year*season*depth)
† log10 transformed data

Table 2.3. Tukey's studentized range test for fecal pellet flux (no./m^2/d) and fecal pellet carbon flux (mg C/m^2/d) collected at station C6B. Means with same letter within each variable are not statistically different at alpha = 0.05

	Number of Samples	Fecal pellet† no.*10^4/m^2/d Means	Fecal pellet carbon† mg C/m^2/d Means
*Year			
1991	60	81.36 A	230.78 A
1992	44	121.83 A	98.55 A
*Season			
Spring	24	102.20 B	350.80 A
Summer	48	20.52 B	42.10 B
Fall	32	212.63 A	236.10 AB
**Depth			
Top Trap ~ 5-6 m	52	40.95 B	229.76 A
Bottom Trap ~ 15 m	52	156.01 A	119.91 B
***Size Fraction			
> 63 µm	52	48.29 B	302.33 A
> 20 µm	52	148.67 A	47.34 B

* test used error-1 = Date(year*season)
** test used error-2 = Date(year*season*depth)
*** test used mean square error
† analysis was performed on log10 transformed data but means are presented as untransformed data

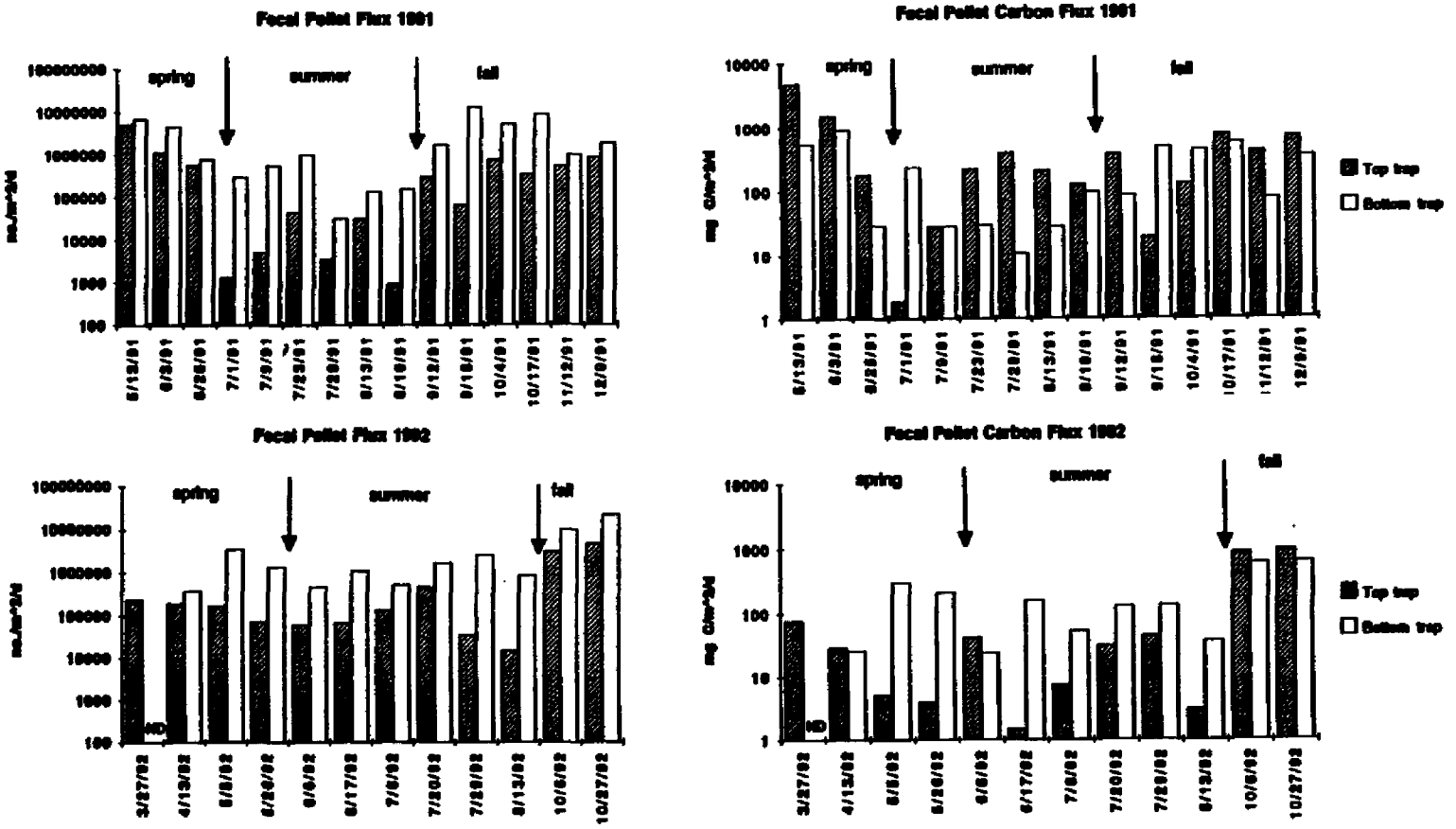


Figure 2.9. Temporal variation in fecal pellet flux (no. m^{-2} d^{-1}) and fecal pellet carbon flux (mg C m^{-2} d^{-1}) collected at 5-6 m (top) and 15 m (bottom) depth at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

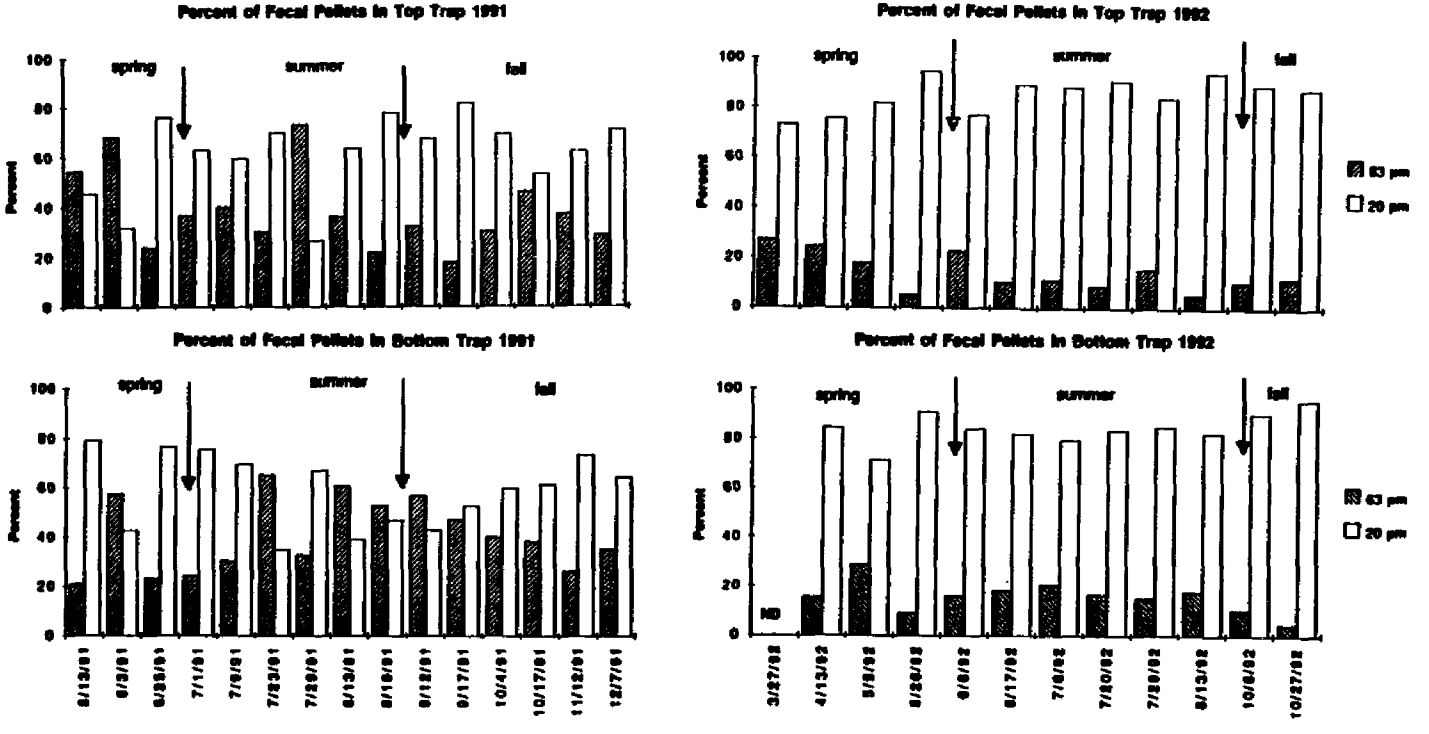


Figure 2.10. Percent of total fecal pellet flux in > 63 µm and > 20 µm size fractions at 5-6 m (top) and 15 m (bottom) depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

consistent across seasons (Fig. 2.9, Appendix B). Depth differences for fecal pellet carbon flux were not significant. Although there was a greater number of smaller (> 20 μm) fecal pellets in both traps in both years (Fig. 2.10), the contribution to the fecal pellet carbon flux by the > 63 μm fecal pellets was much higher compared to the smaller fecal pellets in both years and at both depths (Table 2.3), with a few exceptions (Fig. 2.11).

Fecal Pellet and Fecal Pellet Carbon Fluxes Related to Environmental Variables

The fecal pellet and fecal pellet carbon fluxes in the top trap in 1991 were positively correlated with upper water column dissolved oxygen (DO) and total pigment concentrations (Table 2.4). Elevated concentrations of these hydrographic and biological variables would likely be present in spring, when fecal pellet carbon flux was the highest. Similar relationships were not seen in 1992. The fecal pellet and fecal pellet carbon fluxes in the top trap in 1992 were negatively correlated with delta sigma t, which means that there was less flux during periods of greater stratification. This relationship, however, was not seen in 1991. There were no relationships of fecal pellet flux or fecal pellet carbon flux into the bottom trap in 1991 with any environmental variables examined. Fecal pellet and fecal pellet carbon fluxes into the bottom trap in 1992 were negatively correlated with delta sigma t, as were the top traps. A similar relationship was seen for lower water column salinity, which is probably colinear with sigma t. There were positive relationships between fecal pellet carbon fluxes in the bottom trap in 1992 and upper water column salinity and bottom water dissolved oxygen. No fluxes were correlated with the upper water column salinity lagged one month.

The upper water column total pigment concentration was the best fit predictor variable and explained 33% of the variance for fecal pellet flux and 22% of the variance for fecal pellet carbon flux in 1991. Chlorophyll *a* concentration explained 37% of the

Table 2.4. Pearson correlation coefficients for fecal pellet flux (no. m^{-2} d^{-1}) and fecal pellet carbon flux (mg C m^{-2} d^{-1}) with environmental variables at station C6B during 1991 and 1992, n = 15 and 12 for 1991 and 1992, respectively.

	1991		1992	
	Fecal Pellet (FP) Flux	Fecal Pellet Carbon (FPC) Flux	Fecal Pellet (FP) Flux	Fecal Pellet Carbon (FPC) Flux
Top Trap				
Temp-U	-0.29	-0.27	-0.13	-0.13
Salinity-U	-0.36	-0.51	0.56	0.56
Dissolved oxygen-U	0.72 *	0.78 *	-0.33	-0.36
Delta Sigma t	0.22	0.37	-0.85 *	-0.86 *
Total pigment-U	0.82 *	0.80 *	-0.32	-0.34
Salinity-U¥	0.04	-0.42	0.32	0.31
Bottom Trap				
Temp-U	-0.14	-0.24	-0.28	-0.31
Temp-L	0.25	0.01	0.38	0.47
Salinity-U	0.17	0.08	0.59	0.69 *
Salinity-L	-0.45	-0.43	-0.72 *	-0.66 *
Dissolved oxygen-U	0.15	0.39	-0.24	-0.12
Dissolved oxygen-L	0.42	0.52	0.59	0.79 *
Delta Sigma t	-0.25	-0.03	-0.85 *	-0.91 *
Total pigment-U	0.41	0.31	-0.31	-0.30
Total pigment-L	0.2	0.23	-0.29	-0.42
Salinity-U¥	0.29	-0.16	0.29	0.07

* significant at alpha error = 0.05
U = averaged for surface and 6.5 m depth
L = averaged for 14 m and bottom
Salinity-U¥ = upper water salinity lagged one month

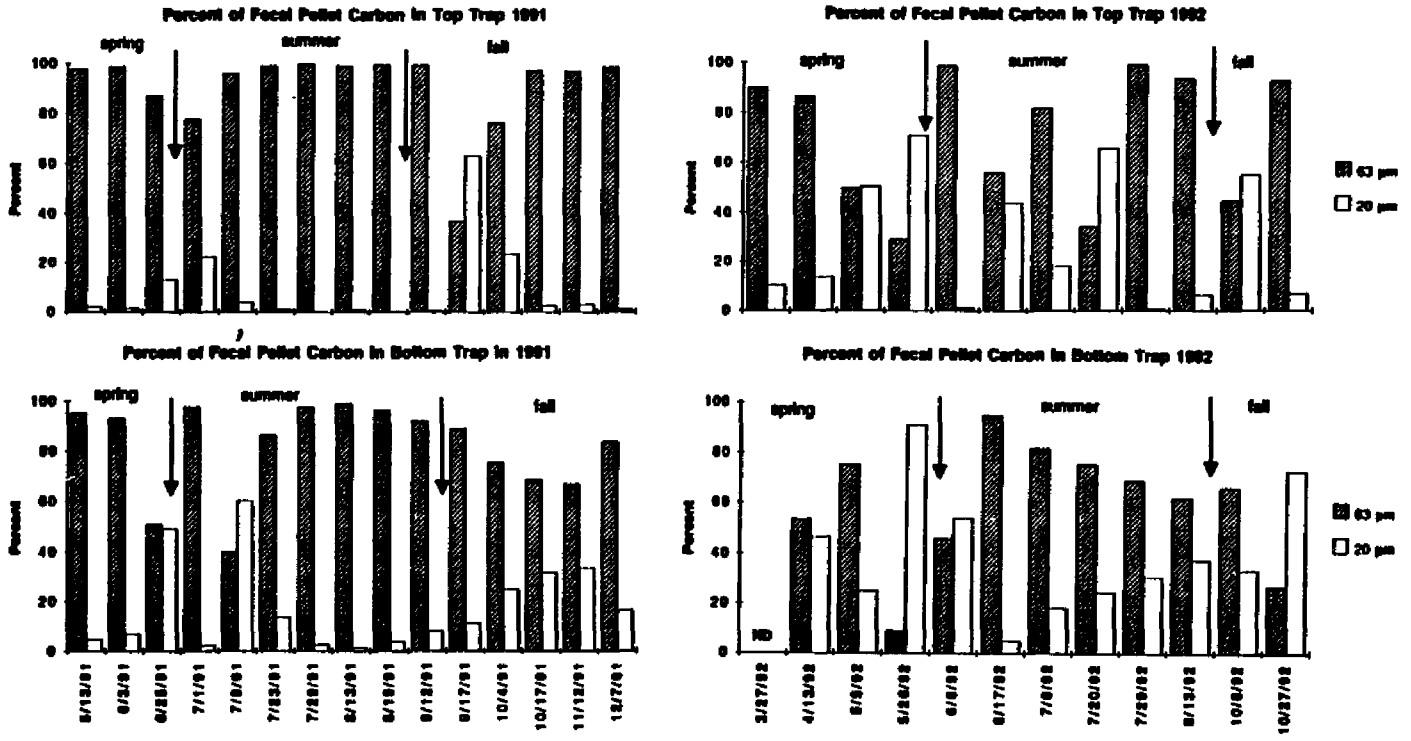


Figure 2.11. Percent of total fecal pellet carbon flux in > 63 µm and > 20 µm size fractions at 5-6 m (top) and 15 m (bottom) depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

variability for fecal pellet carbon flux. The lower water column dissolved oxygen was positively related with the bottom trap fecal pellet and fecal pellet carbon fluxes in 1991 and explained 61% and 63% of the variances, respectively (Table 2.5).

The upper water column salinity and delta sigma t were negatively related and each explained 18% and 67% of variance for fecal pellet flux, and 24% and 60% of the variance for fecal pellet carbon flux in the top trap in 1992. Delta sigma t was negatively related to fecal pellet and fecal pellet carbon fluxes and explained 88% and 64% of the variances in the bottom trap in 1992 (Table 2.5).

Fecal Pellets in Surficial Sediments

Fecal pellet abundance in surficial sediments in 1991 generally increased progressively from winter through spring and summer, then decreased in fall (Fig. 2.12). Fecal pellet abundance in 1992 did not follow the same pattern, but was generally high throughout spring, increased in May, then declined in summer and fall (Fig. 2.12).

The differences in surficial sediment fecal pellets between years and seasons were not significant (Tables 2.6 and 2.7), but the year*season interaction was significant. There were more fecal pellets in the > 20 μm size fraction than in the > 63 μm size fraction, and there was a significant year*size fraction interaction. Surficial sediment fecal pellets in the > 20 μm size fraction were more abundant compared to the > 63 μm size fraction in all seasons in 1991. Larger fecal pellets (> 63 μm) were more numerous in spring 1992, but smaller fecal pellets dominated later in the year (Fig. 2.13).

The surficial sediment fecal pellet carbon was not significantly different between years, but there were significant seasonal differences and a significant year*season interaction (Tables 2.6 and 2.7). Spring and summer were significantly higher than fall (Table 2.7). Fecal pellet carbon was significantly higher in the > 63 μm

Table 2.5. Best fit linear regressions for fecal pellet flux (no./m^2/d) and fecal pellet carbon flux (mg C/m^2/d) at 5-6 m (top trap) and 15 m (bottom trap) depths with environmental variables from station C6B during 1991 and 1992.

Flux	Model	P > F	r^2	n
1991				
Top trap (5-6 m)				
log fecal pellet	= 10.2 + 2.5 log total pigment-U	0.0796	0.33	15
log fecal pellet carbon	= 5.4 + 2.3 log chlorophyll a-U - 1.4 log total pigment-U	0.0405*	0.60	15
Bottom trap (15 m)				
log fecal pellet	= 11.22 + 2.2 log DO-L	0.0061*	0.63	15
log fecal pellet carbon	= 2.9 + 1.64 log DO-L	0.0079*	0.61	15
1992				
Top trap (5-6 m)				
log fecal pellet	= 66.9 - 13.2 log salinity-U - 4.92 log delta sigma t	0.0015*	0.84	12
log fecal pellet carbon	= 80.2 - 18.9 log salinity-U - 6.2 log delta sigma t	0.0018*	0.84	12
Bottom trap (15 m)				
log fecal pellet	= 19.6 - 2.7 log delta sigma t	0.0002*	0.88	11
log fecal pellet carbon	= 8.84 + 2.11 log delta sigma t	0.0042*	0.64	11

* significant at alpha = 0.05
U = averaged for surface and 6.5 m depth
L = averaged for 14 m and bottom

Table 2.6. Split plot design ANOVA for analysis of variance for fecal pellets (no./m^2) and fecal pellet carbon (mg C/m^2) in surficial sediments at station C6B during 1991 and 1992.

Sources	df	Fecal Pellets P > F	Fecal Pellet Carbon** P > F
Model	26	0.0219*	0.0001*
Error	15		
***Main Plot			
Year	1	0.0962	0.1481
Season	2	0.2931	0.0212*
Year*Season	2	0.0011*	0.0038*
Error-1	15	0.3605	0.0586
Sub plot			
Size Fraction (SF)	1	0.0021*	0.0001*
Year*SF	1	0.0496*	0.5311
Season*SF	2	0.2803	0.1122
Year*Season*SF	2	0.5623	0.0303*

* significant at alpha error = 0.05
** log10 transformed data
*** test of hypothesis used error-1 = Date(Year*Season)

Table 2.7. Tukey's studentized range test for fecal pellets (no./m^2) and fecal pellet carbon (mg C/m^2) in surficial sediments at station C6B. Means with same letter within each variable are not statistically different at alpha = 0.05.

	Number of Samples	Fecal Pellets (no.*10^7/ m^2)	†Fecal Pellet Carbon (mg C /m^2)
*Year			
1991	22	2.45 A	2392 A
1992	20	2.39 A	4925 A
*Season			
Spring	22	2.55 A	4022 A
Summer	10	2.48 A	4551 A
Fall	10	2.09 A	1714 B
**Size Fraction(SF)			
> 63 µm	21	3.04 A	6325 A
> 20 µm	21	1.81 B	872 B

* test used error-1 = Date(year*season)

** test used mean square error

† analysis was performed on log10 transformed data but means are presented as untransformed data

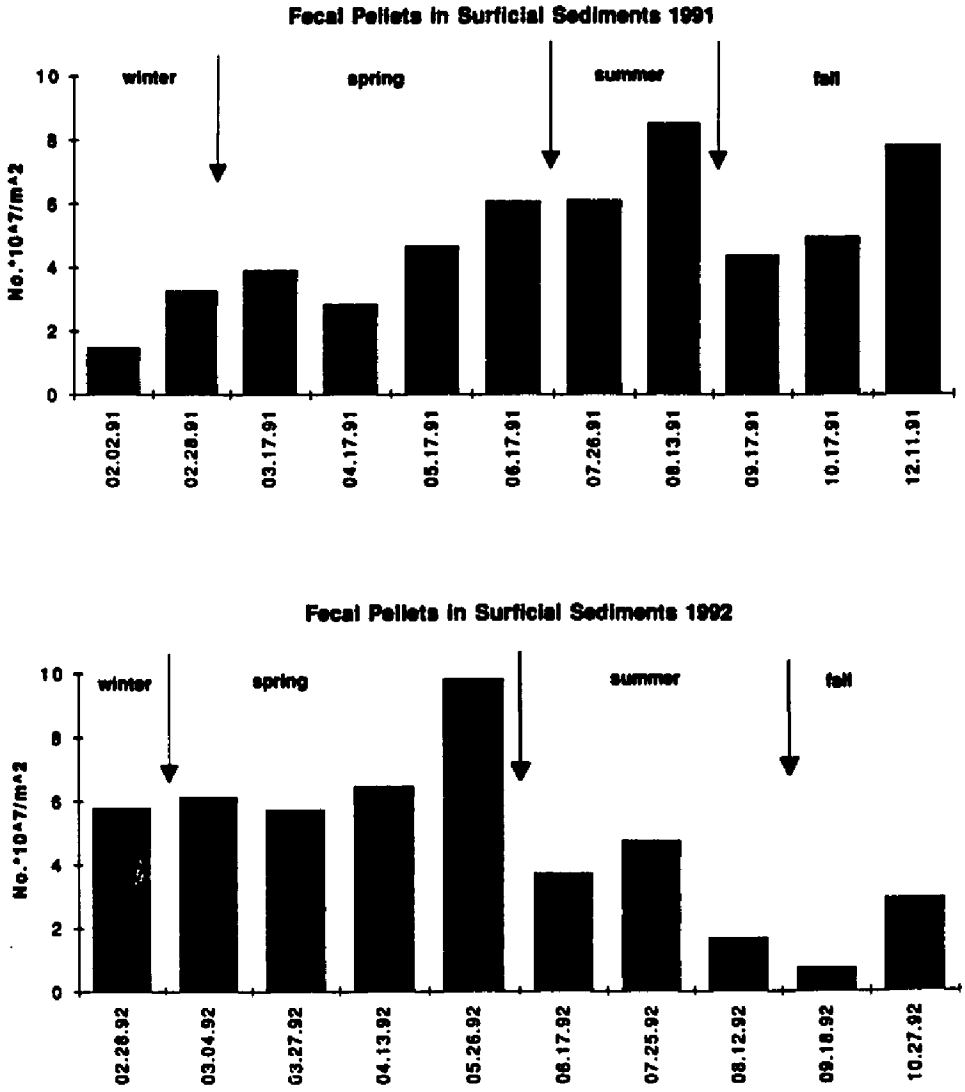


Figure 2.12. Temporal variation in the abundance of fecal pellets (no. m^{-2}) in surficial sediments in the vicinity of the sediment trap mooring (station C6B) during 1991 and 1992. Arrows delineate dates included in each season.

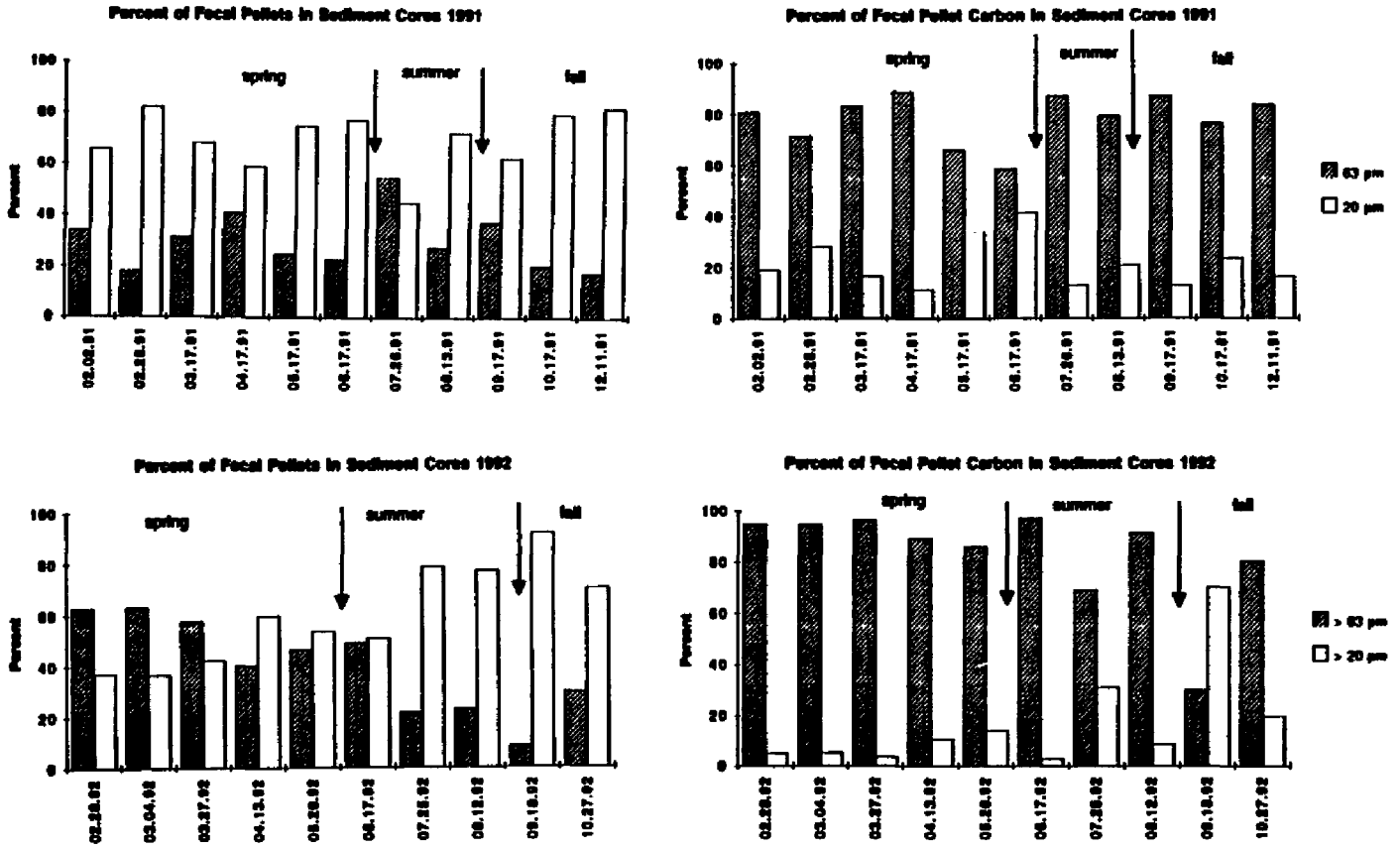


Figure 2.13. Percent of total fecal pellets and total fecal pellet carbon in > 63 µm and > 20 µm size fractions in surficial sediments in the vicinity of sediment trap mooring (station C6B) collected during 1991 and 1992. Arrows delineate dates included in each season.

size fraction than in the > 20 μm size fraction. Although there were more smaller (> 20 μm) fecal pellets in the surficial sediments, larger (> 63 μm) fecal pellets contributed more carbon in both years with the exception of one sample (September 18, 1992) (Fig. 2.13). Surficial sediment fecal pellet carbon (Fig. 2.14) followed a similar trend to that of fecal pellet number for both years (Fig. 2.12).

Relationships of Sediment Fecal Pellets and Fecal Pellet Carbon with Environmental Variables

There were no significant differences in sediment total pigment concentration, %TOC, and sediment grain size distribution between years, seasons, and the year*season interaction (single factor ANOVA) (Table 2.8). Phaeopigments comprised most of the total pigments in the sediments, and chlorophyll *a* was usually found in the spring and summer (Fig. 2.15). The %TOC in the sediments was low, and averaged 0.91 (± 0.33 SD) (Fig. 2.16). The sediment grain size averaged 13% sand, 84% silt and 3% clay (Fig. 2.16). The fecal pellet carbon in sediments was positively correlated with sediment chlorophyll *a* (Table 2.9), which pointed to fecal pellets as a potential source of chlorophyll *a* in the sediments.

Fecal pellet carbon in the sediments in 1991 increased with a decrease of dissolved oxygen in summer and decreased in fall with an increase in dissolved oxygen caused by a mixing of the water column after a series of frontal passages (Fig. 2.14). The negative relationship of fecal pellets with bottom water dissolved oxygen, however, was not significant (Table 2.9), but may indicate an accumulation of fecal pellets during summer when currents are minimal. There was no clear trend in 1992 for similar data (Fig. 2.14).

The number of fecal pellets in the sediments was positively correlated with bottom water salinity (Table 2.9). Both fecal pellet numbers and carbon were negatively related to bottom water temperature in 1991. Lowest bottom water

Table 2.8. Analysis of variance results (P > F) for total pigment (μg/g dry wt), %TOC and grain size collected from station C6B during 1991 and 1992.

Variables	df	Total pigments P > F	%TOC P > F	%sand P > F	%silt P > F	%clay P > F
Model	5	0.1703	0.9471	0.6385	0.4628	0.1475
Year	1	0.2597	0.7477	0.1651	0.1035	0.6735
Season	2	0.7048	0.7677	0.5423	0.3696	0.3201
Year*Season	2	0.1503	0.8942	0.5838	0.7932	0.0871

* significant at alpha error = 0.05

Table 2.9. Pearson correlation coefficients matrix of fecal pellet (no./m^2) and fecal pellet carbon (mg C/m^2) with sediment and bottom water environmental data for 1991 and 1992, n = 11 and 10, respectively.

	1991		1992	
	Fecal Pellets no./m^2	Fecal Pellet Carbon g C/m^2	Fecal Pellets no./m^2	Fecal Pellet Carbon g C/m^2
Sediments				
Chlorophyll a (µg/g dry wt)	-19.00	-0.27	-0.03	0.75 *
Phaeopigment (µg/g dry wt)	-0.13	0.01	-0.24	0.34
Total pigment (µg/g dry wt)	-0.14	-0.03	-0.20	0.46
%TOC	-0.13	-0.33	0.07	-0.49
% Sand	-0.06	0.09	0.74 *	0.4
%Silt	-0.10	-0.09	-0.74 *	-0.38
% Clay	-0.05	-0.05	-0.74 *	-0.59
Bottom Water				
Temperature (°C)	0.32	0.52	-0.65 *	-0.62 *
Salinity (ppt)	0.15	0.37	0.62 *	0.56
Dissolved Oxygen (mg/l)	-0.39	-0.57	0.04	-0.23
Delta sigma t	-0.36	-0.03	0.25	0.45
Total pigment (µg/l)	-0.18	-0.46	-0.29	-0.32

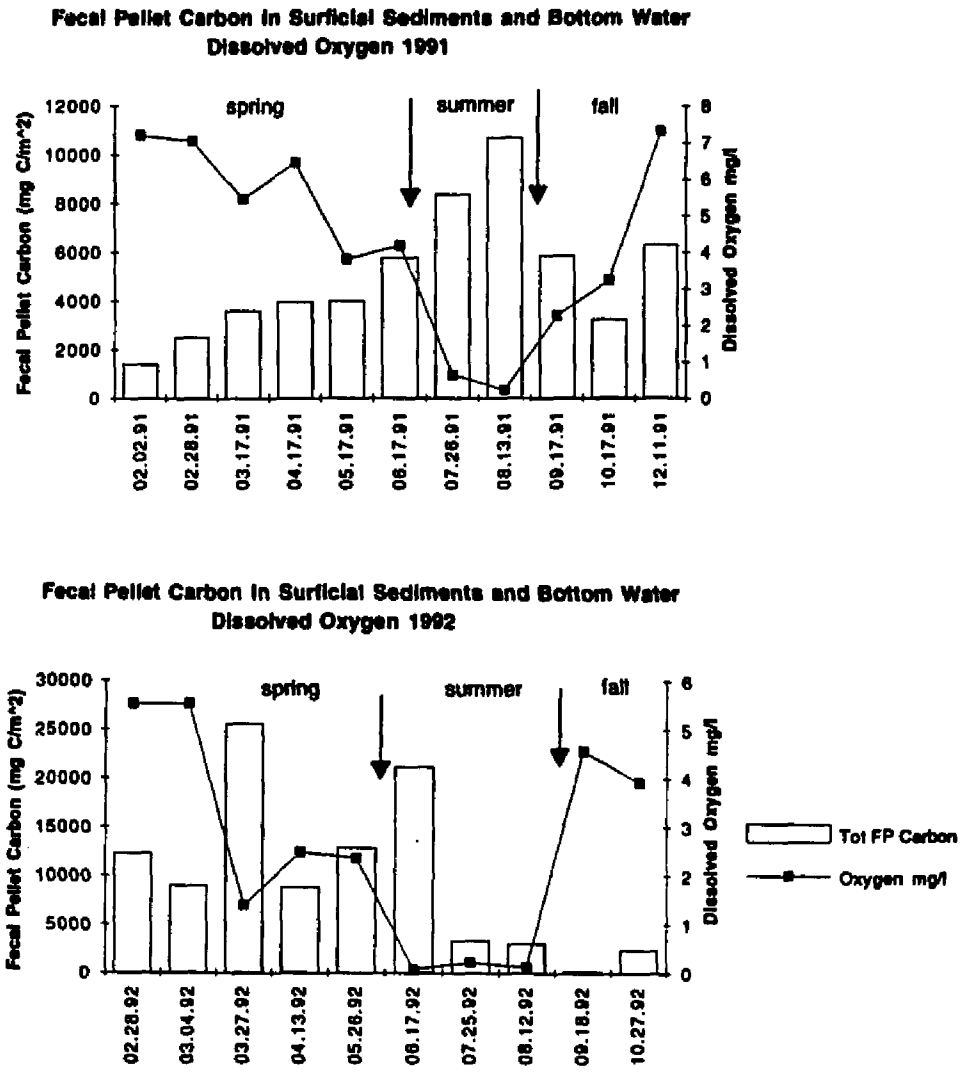


Figure 2.14. Temporal variation in fecal pellet carbon (mg C m^{-2}) in surficial sediments in the vicinity of sediment trap mooring (station C6B) and bottom water dissolved oxygen (mg l^{-1}) during 1991 and 1992. Arrows delineate dates included in each season.

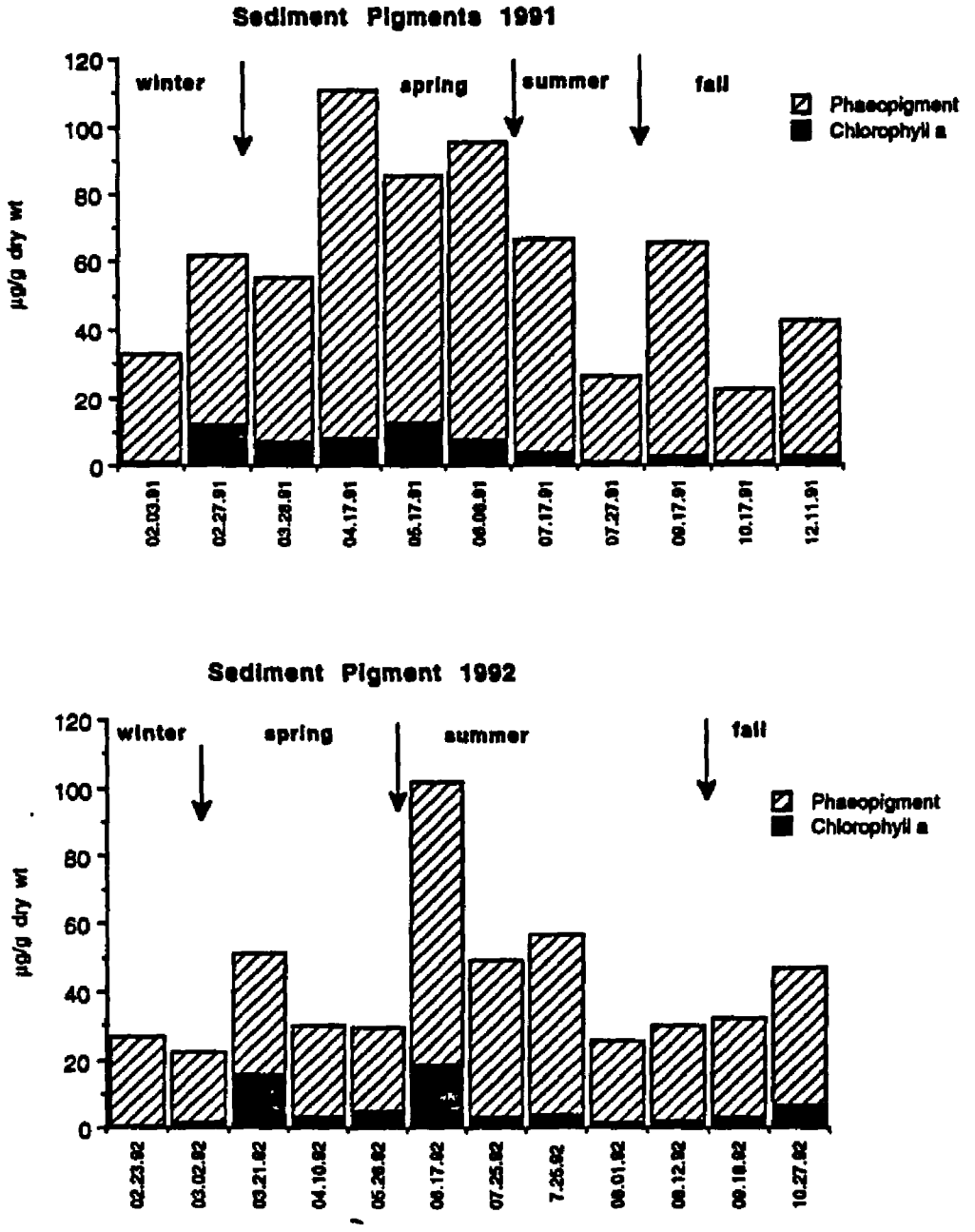


Figure 2.15. Temporal variation in sediment total pigment concentrations (chlorophyll *a* and phaeopigment are stacked to show total pigments) (µg g^{-1} dry weight) collected from the vicinity of the sediment trap mooring (station C6B) during 1991 and 1992. Arrows delineate dates included in each season.

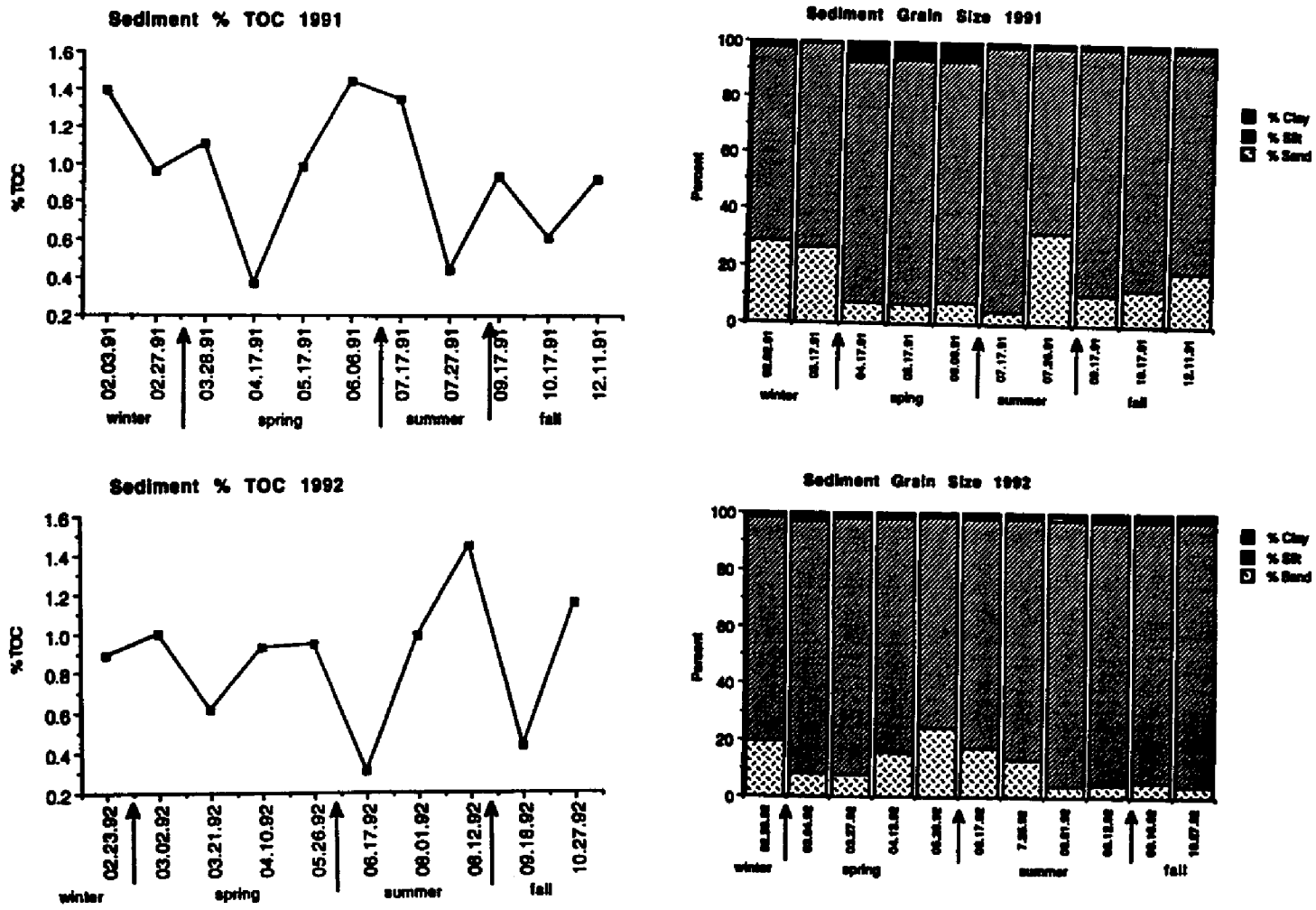


Figure 2.16. Temporal variation in sediment percent total organic carbon (%TOC) and grain size distribution in the vicinity of the sediment trap mooring during 1991 and 1992. Arrows delineate dates included in each season.

temperatures are likely to occur in winter and spring, when resuspension events would be more frequent.

The best fit predictor model for fecal pellet and fecal pellet carbon in the sediments with bottom water variables and sediment characteristics identified a negative relationship with water column phaeopigment, which explained 60 to 51% of the variances, respectively in 1991 (Table 2.10). Fecal pellets in 1992 were negatively related with temperature (17% variability based on partial r^2) and positively with %sand (55% variability based on partial r^2). The sediment fecal pellet carbon was also negatively related with temperature (34% variability based on partial r^2) and positively related with sediment chlorophyll *a* (57% variability based on partial r^2) (Table 2.10).

Resuspension Potential of Fecal Pellets

The measured currents at 1 m above the seabed from May 10 to August 24, 1992 (W. J. Wiseman, Jr. unpubl. data) ranged from 3 to 30 cm s^{-1}, and in only 2-3 short intervals, currents were > 30 cm s^{-1} (Appendix A). The average currents in May were ~ 10 cm s^{-1}, decreased to ~ 5 cm s^{-1} in June and were ~ 10 cm s^{-1} in July through August (Fig. A.1). Fecal pellets would likely be resuspended for a large part of the mid-summer 1992 record, because fecal pellets may be resuspended at current speeds > 7 cm s^{-1} (Table A.2). The disposition or fate of winnowed fecal pellets is not known. The likelihod of resuspension and transport increases with the increased frequency of cold front passages in fall through spring.

DISCUSSION

Temporal Variability

The average fecal pellet carbon flux for two years was high (229.8 mg C m^{-2} d^{-1} at ~5-6 m and 119.9 mg C m^{-2} d^{-1} at 15 m depth) (Table 2.3), and was among the

Table 2.10. Best fit linear regressions for fecal pellet (no. /m^2) and fecal pellet carbon (mg C/m^2) in surficial sediments with environmental variables from station C6B during 1991 and 1992.

Flux	Model	P > F	r^2	n
1991				
log fecal pellet	= 7.9*10^7 - 1.7*10^7 log phaeopigment-B	0.0232*	0.60	15
log fecal pellet carbon	= 8617 - 1945 log phaeopigment-B	0.0197*	0.51	15
1992				
log fecal pellet	= 11.9*10^7 - 4.4*10^7 log temperature-B + 2.2*10^7 log sand	0.0110*	0.74	14
log fecal pellet carbon	= 45042 - 1843 log temperature-B + 984 sediment chlorophyll a	0.0003*	0.91	14

* significant at alpha = 0.05
B = bottom (19 m)

higher values reported for fecal pellet carbon flux in coastal waters (Table 2.11). Although there were no statistical differences in fecal pellet carbon flux between years (Tables 2.2 and 2.3), fluxes were considerably different between years. Fluxes varied seasonally, and the year*season interaction was significant (Tables 2.2 and 2.3).

The spring freshet of the Mississippi River was much lower in 1992 (10,000-20,000 $m^3 s^{-1}$) than in 1991 (20,000-35,000 $m^3 s^{-1}$) at Tarbert Landing, Mississippi (Dinnel 1993). Hydrographic features of the Louisiana inner shelf vary with inter-annual differences in river discharge, and also on shorter time scales due to changes in winds, fronts, and circulation patterns (Rabalais et al. 1992). Changes in the hydrographic regime, movement of water masses, stratification, and nutrient availability likely influence temporal and spatial changes in species composition of phytoplankton as well as zooplankton communities (Maita et al. 1988). The phytoplankton species composition changes primarily from large heavily or moderately silicified diatoms to lightly silicified diatoms, and later to non-diatom communities (Dortch et al. 1992). A temporal succession in zooplankton communities was also observed in a less extensive sampling program concomitant with this study (Chapter 4).

High fecal pellet flux has been reported to occur in the water column when surface productivity rates are high (Knauer et al. 1979). Fecal pellet carbon flux was very high in the top trap in spring and summer 1991, due largely to larger, tubular fecal pellets, which were usually broken pieces of much longer fecal pellets. Producers of these large tubular fecal pellets were unknown but were probably larger mesozooplankton (holoplankton or meroplankton > 300 mm). A linkage between fecal pellet carbon flux and surface water productivity (positive correlations with dissolved oxygen and total pigments, Table 2.4) suggests that much of the phytoplankton production was stimulated by the higher spring flow in 1991 and was exported from the surface layer to the bottom layer via fecal pellets. Average annual and peak spring river flow were lower in 1992 than in 1991 (Fig. 1.2). There were no statistically significant

Table 2.11. Comparison of fecal pellet flux and fecal pellet (FP) carbon flux in shallow water areas.

Systems	Depth m	Fecal Pellet Flux (no.*10^3/m^2/d)	FP Carbon Flux (mg C/m^2/d)	Reference
Northern Pacific Open Ocean	35-150	203-324	15.1-34.1	Urrere & Knauer 1981
Northern Pacific Coast	50-250	17.1-22	0.84-0.96	Knauer et al. 1979
Coastal Upwelling	50-250	219-318	28-38	
Open Ocean	75	1.36	0.07	
Dabob Bay, Puget Sound	50-80	520-14000		Shuman 1978
Santa Barbara Basin	430-570	244-333	200	Soutar et al. 1977
Northwestern Mediterranean	50-250	10-7000	1-140	Fowler et al. 1991
Northern Adriatic Sea	27	1810-2710		Bochdansky & Herndl 1992
Chirikov Basin Northern Bering Sea	13-26		153.4-390.4	Fukuchi et al. 1993
Inner Continental Shelf	*5 to 6*	*4.45-5900*	*238-3148*	*This study*
Gulf of Mexico	*15*	*31.6-12900*	*387-411*	

correlations between either the upper water column total pigment concentrations or dissolved oxygen and the top trap fecal pellet carbon fluxes in 1992 as there were in 1991. The fecal pellet and fecal pellet carbon fluxes into both traps were negatively correlated with delta sigma t, the index of density stratification, which also explained a significant portion of the variability. These relationships indicate that high fluxes occurred when the water column was mixed (Tables 2.4 and 2.5). The results are consistent with the findings of Knauer et al. (1979), Maita et al. (1988) and Miquel et al. (1994).

The seasonal variability in the contribution of fecal pellets to carbon flux is controlled by the degradation of fecal pellets and by the content of fecal pellets, that in turn is affected by food availability. A decrease in food availability has been related to gut fullness and a decrease in production of fecal pellets (Paffenhofer & Knowles 1979, Dagg & Walser 1986). Fecal pellets produced under low food conditions are smaller, fragile, and have low sinking rates (Small et al. 1979, 1987). Smaller fecal pellets with slower sinking rates and increased potential for decomposition under higher temperature regimes may contribute to significant loss of fecal pellets in summer. Similar processes may explain some of the seasonal differences seen in this study. Both fecal pellet flux and fecal pellet carbon flux were lowest in summer in this study.

Most (> 80%) of the fecal pellets in fall were small (> 20 μm). The presence of more smaller fecal pellets (> 20 μm) than larger fecal pellets (> 63 μm), especially in fall (Table 2.3), was comparable to Bathmann & Liebezeit (1986) and Qureshi et al. (1992). Recently, however, Urban (1992) discussed the contents of fecal pellets and fecal pellet compactness and dynamic density (density that is controlled by the compactness of the component particles), that in turn affect sinking rates of fecal pellets. Changes from a diatom based food chain in the spring to a microbial loop-based food chain in the fall were observed in the contents of copepod (*Calanus finmarchicus)* and oikopleura (*Oikopleura vanhoeffeni*) fecal pellets in Conception Bay,

Newfoundland (Urban et al. 1992). The fecal pellets produced during the fall were filled with bacteria and ciliates indicating the importance of the microbial loop in either direct feeding on these particles or feeding on aggregated particles or 'marine snow'. The compactness of fecal pellets, contrary to density of the components (Bienfang 1980), appears to influence fecal pellet density (Urban 1992). The seasonal variation in fecal pellet dynamic density, therefore, has important implications for vertical particulate carbon flux, because there can be two or more populations of fecal pellets in spring, summer, and fall with different potentials for settling related to food availability (Urban 1992). Voss (1991) speculated that ingestion of athecate phytoplankton may lead to production of fragile, sparsely packed fecal pellets with a lower sinking velocity in comparison to densely packed fecal pellets with remains of dinoflagellate thecae or diatoms. Therefore, without major changes in grazing pressure, a shift in the phytoplankton population can potentially lead to different fecal pellet populations with differences in morphology, density and settling velocity and resulting in increasing or decreasing fecal pellet contribution to the total flux of carbon (Voss 1991).

More smaller (20 μm) fecal pellets in the fall may likely be due to a change in phytoplankton species composition from highly silicified diatoms to lightly silicified diatoms with seasonal decreases in silicate availability (Figs. 2.5 and 2.6). A temporal difference in species composition was also observed in the phytoplankton flux from higher flux of diatoms in spring in comparison to summer and fall when cyanobacteria dominated the flux in the hypoxic region (Dortch et al. 1992).

Depth Related Variability

There was significantly greater fecal pellet flux into the bottom trap than into the top trap, although the fecal pellet carbon flux was higher in the top trap largely because of the presence of larger tubular fecal pellets (Table 2.3). The lower trap collected more fecal pellets than the top trap, in part, because it integrated over a greater

depth. Additonal considerations are that there may have been more fecal pellets being produced below the depth of the top trap near the pycnocline, zooplankton might act as 'biological pumps' by feeding at the surface and defecating in the deeper waters, and resuspended fecal pellets may have fallen into the bottom trap.

Fecal pellets collected in the bottom trap may have originated from feeding activities in sub-pycnocline waters where entrainment of particles is likely (Dagg et al. 1988, Walsh et al. 1988, Gardner 1989, Youngbluth et al. 1989). Entrainment of particles at a density gradient may result in feeding activities at that depth so more fecal pellets were found below the pycnocline where organisms were feeding. The total fecal pellet concentrations were higher in the bottom waters and were positively related to the concentrations of copepod nauplii (Chapter 5). High copepod abundances at station C6B in the bottom waters may be due to the ability of copepods to remain within food layers. A bimodal distribution of pellet flux has been reported (Bishop et al. 1980, Urrere & Knauer 1981, Sakasi et al. 1988, Ayukai & Hattori 1992), and has been attributed to *in situ* fecal pellet production by microbial organisms, and mesozooplankton populations present at depth, or by lateral advection of particles to the area (Karl et al. 1984, Karl & Knauer 1984, Ayukai & Hattori 1992).

Larger string-shaped fecal pellets of krills and salps and fish fecal material are found in sediment traps from various regions (Staresinic et al. 1983, Iseki 1981, Madin 1982, Matsueda et al. 1986). Larger fecal pellets usually sink out of the upper water column rapidly at rates on the order of 10^2 to 10^3 m d^{-1} (Madin 1982). Larger organisms produce larger fecal pellets (Paffenhofer & Knowles 1979, Maita et al. 1988). About 15% of the fecal pellets in spring and summer of 1991 were tubular and larger than 300 μm. This difference in pellet size could be due to larger dominant organisms present during the period. The zooplankton community can thus affect the vertical carbon flux from the surface waters to the bottom. Youngbluth et al. (1989) observed high densities of euphausiid, *Megayctiphanes norvegica*, fecal pellets

coincident with a pycnocline. These large, cylindrical, rapidly sinking pellets contributed substantial amounts of organic material transported to the bottom. The fecal pellet flux was higher in the bottom trap than in the top trap, with more smaller (> 20 μm) fecal pellets compared to larger (> 63 μm) fecal pellets at both depths (top and bottom) (Table 2.3). Fecal pellet carbon flux, however, was greater in the top trap than in the bottom trap, and apparently, the larger size fraction fecal pellets (> 63 μm) contributed more carbon to the total fecal pellet carbon flux than the smaller fecal pellets (> 20 μm). Thus, the larger fecal pellets dictated the carbon flux to the seabed.

Larger fecal pellets do not always sink out of the euphotic zone. They can also be retained and remineralized in the water column due to mechanical breakup, coprorhexy, coprochally (Lampitt et al. 1990, Noji 1991), coprophagy (Paffenhofer & Knowles 1979, Lampitt et al. 1990, Noji 1991), and bacterial decomposition (16 to 67 percent in two days, Turner 1979). It has been suggested that pellets may not be able to sink rapidly out of the upper water column if they have a large volume relative to their specific weight (e.g. salp pseudofeces, Madin 1982) or low density (Bruland & Silver 1981, Deibel 1990). The presence of greater number of larger fecal pellets in the top trap in spring and summer may be due to a combination of all factors listed above and a certain hydrographic regime, for example a stratified water column, which can be responsible for retention of fecal pellet in the euphotic zone, thus influencing the carbon flux by retention and decreasing the sedimentation of larger as well as smaller, fecal pellets (Bathmann et al. 1987).

Mesozooplankton may act as a 'biological pump' by feeding at the surface and defecating at depths below the upper water layer (Turley 1992, Longhurst & Harrison 1988). This process would result in collection of fewer fecal pellets in a trap in the upper water column and possibly more at depth.

More smaller (> 20 μm) fecal pellets in the bottom trap in the fall may be due to resuspension events. The limited current meter record from mid-summer of 1992

indicated several periods where bottom currents were greater than 7 cm s^{-1} (Table A.2) and capable of resuspending fecal pellets. Whether these fecal pellets would be resuspended well up into the water column or winnowed away from the area is not known. The resuspension of fecal pellets and transport from the area would be more likely to occur during spring and fall when fronts are more frequent in comparison to summer when winds are relatively calm and the water column is more stable.

The fecal pellets in surficial sediments were similar in size, shape and appearance to those found in the traps. Although benthic organisms cannot be ruled out as a source, the fecal pellets found in the sediments appear to be derived from the water column. The seasonal differences in the number of fecal pellets and fecal pellet carbon flux in the surficial sediments was not significant because of high variability. However, there were considerably more fecal pellets in surficial sediments in spring and summer compared to fall (Table 2.7). The accumulation rate of fecal pellets in the surficial sediments was not known. However, if fecal pellet flux is greater in spring (Table 2.3), the likelihood of accumulation in the sediments in spring is greater. Resuspension events are likely to occur in spring, but the magnitude of the flux of fecal pellets may exceed the resuspension and transport of fecal pellets from the area. Comparison with oxygen data indicates fecal pellets were more numerous in summer in 1991 (Fig. 14), when bottom waters were more stagnant, which allowed for accumulation of fecal pellets over time. Sediment cores with as much as 1 cm of fecal pellets overlying the sediment surface were collected from station C6B in mid-summer 1990 (N. N. Rabalais pers. comm.). There was no clear trend in increase in fecal pellet accumulation through summer in 1992; however, it is likely that fecal pellets were resuspended during periods when bottom currents exceeded the critical velocity for fecal pellet resuspension (Table A.2). Lower numbers of fecal pellets in sediments in fall likely result from resuspension events during cold front passages. Strong currents from the passage of Hurricane Andrew through the study area in August 1992 removed as much as 8 cm of

the finer, less compacted surface sediments (N. N. Rabalais pers. comm.). Finally, fecal pellet utilization by benthic organisms is likely to be greater in spring and fall than in summer, when numbers of the usual surface deposit feeding benthic community are drastically reduced due to severely hypoxic bottom waters (Rabalais et al. 1993).

There were significantly more larger (> 63 μm) fecal pellets in the surficial sediments (Table 2.8), which could be due to remineralization of smaller fecal pellets within the water column relative to larger fecal pellets. Other possibilities include resuspension and winnowing of smaller fecal pellets from the sediment surface, selective utilization of smaller fecal pellets by benthic organisms, or the faster sinking rates of larger fecal pellets.

CONCLUSIONS

Sediment traps were deployed in 20 m water depth on the continental shelf under the influence of the Mississippi River within an area of chronic and seasonally severe hypoxia. Surface and bottom water layers, as well as surficial sediments, were sampled over two years to determine the variation in fecal pellet number and quality, as well as fecal pellet carbon.

The size and shape of fecal pellets collected in the sediment traps and knowledge of the meso- and microzooplankton communities in the study area (Chapters 4 and 5) indicated that the fecal pellets in the traps were likely produced by the dominant zooplankters, copepods and larvaceans. The mid-sized, ellipsoidal fecal pellets were the most abundant and were probably an important component of fecal pellet carbon flux. Larger, tubular fecal pellets, however, were occasionally abundant and periodically influenced the carbon flux values.

There was considerable inter-annual and temporal variability in the fecal pellet number and carbon flux. The numbers collected in the top and bottom traps ranged

from $1.5*10^4$ to $4.7*10^6$ m^{-2} d^{-1} and from $2.1*10^4$ to $2.2*10^7$ m^{-2} d^{-1}, respectively. Carbon fluxes as fecal pellets ranged from 1.5 to 4818 mg C m^{-2} d^{-1}, were highest in the spring and lowest in the summer with fall being intermediate. Fecal pellet carbon flux was also higher in 1991 than in 1992, but the difference was not statistically significant. More fecal pellets were collected in the bottom trap compared to the top trap. A greater percentage of smaller fecal pellets were collected at both depths compared to larger fecal pellets. The highest fecal pellet carbon flux, however, was accounted for by the larger pellets. Larger fecal pellets dominated in the surficial sediments. While the numbers of fecal pellets in the sediments did not differ between seasons, the carbon attributed to these pellets was significantly greater in spring and summer than in fall.

Fecal pellet number and carbon fluxes were positively correlated with indicators of high surface water productivity (dissolved oxygen and total pigment concentrations) in 1991, but not in 1992. Fecal pellet carbon fluxes into the top trap in 1991, and into the top and bottom traps in 1992, were negatively correlated with delta sigma t. No clear relationships with bottom water features or sediment characteristics were evident for sediment fecal pellet numbers or carbon estimates. Resuspension of fecal pellets would likely occur for a large portion of mid-summer 1992 based on calculations of critical velocity from a limited current meter record. The disposition or fate of winnowed fecal pellets is not known.

I had hypothesized that the summertime flux of fecal pellets would exceed that of spring and summer, because a mature zooplankton population would likely produce larger fecal pellets that would sink quickly out of the upper layers. Instead, fecal pellet carbon fluxes were highest in spring, followed by fall, and were much lower in summer. Comparison of the flux data with water column hydrographic data indicated that fecal pellet carbon flux was greater during periods of higher surface water production (as indicated by high dissolved oxygen and pigment concentrations). These conditions dominate in spring. Higher fecal pellet carbon flux in 1991 compared to

1992 can also be linked to productivity in the surface waters, because the spring freshet of the Mississippi River was much greater in 1991 than in 1992. The number and flux of fecal pellets in the spring are likely directly related to food availability and high phytoplankton biomass stimulated by the nutrient rich Mississippi River waters. The lower flux of fecal pellets in summer may be due to reduced food availability. Fecal pellet and fecal pellet carbon fluxes in 1992 were negatively correlated with delta sigma t, a measure of the strength of stratification. This relationship indicates less flux during periods of greatest stratification and water stability (i.e., summer) and higher fluxes during periods when the water column was mixed. Lower fluxes in summer may be due to retention or remineralization of fecal pellets in the upper water column, or less likelihood of resuspension than in the spring and fall during mixing events. Spring fecal carbon flux exceeded fall, although resuspension might occur during both seasons. The higher values in spring, however, are more likely related to food availability, because phytoplankton biomass in the surface waters is generally higher than in fall. Further evidence for seasonal differences in flux through the water column was seen in the seasonal differences in fecal pellet carbon in the surficial sediments. Both spring and summer sediment fecal pellet carbon were much higher than in the fall. Flux through the water column was greater in spring, and accumulation in the sediments probably exceeded resuspension and transport from the area. Summertime accumulation of fecal pellets in the surficial sediments was facilitated by minimal bottom currents, although some fecal pellets would be resuspended but may not be transported. The much lower fall sediment fecal pellet carbon might represent less flux (i.e., less food availability) as well as resuspension and transport from the area from elevated currents during passage of cold fronts.

More fecal pellets were collected in the bottom trap compared to the top trap, which is likely due to depth integration, entrainment of particles at the pycnocline, zooplankton acting as 'biological pumps', and or collection of resuspended material in

the bottom trap. Fecal pellet carbon flux was dominated by larger particles, as I had predicted, but the percentage of smaller fecal pellets actually exceeded that of the larger size fraction. Larger fecal pellets dominated in the surficial sediments, possibly due to winnowing of smaller fecal pellets or selective utilization by benthic organisms.

The greatest potential for sinking of organic material derived from *in situ* production exists in the spring in response to increased phytoplankton production which is stimulated by riverine nutrient delivery. These fluxes may be directly as phytoplankton cells, or indirectly as fecal pellets and aggregates (which may include phytoplankton cells as well as fecal pellets). The seasonal progression of whole versus repackaged (as pellets) phytoplankton for both years of this study is not known. However, comparisons of phytoplankton cell carbon flux derived from cell volume to carbon content ratios (Q. Dortch pers. comm., Chapter 3) showed that the flux of carbon in fecal pellets was an order of magnitude greater than phytoplankton cell carbon flux for both top and bottom traps in 1991. A massive flux of ungrazed phytoplankton cells from high surface production in the spring cannot be ruled out, but the flux calculations for the spring through fall period of 1991 indicated that fecal pellet carbon flux far exceeded the contribution of carbon to the seabed by phytoplankton cells. The relative contribution of phytoplankton carbon versus fecal pellet carbon to organic matter flux is not yet determined for trap data collected earlier in 1992 (beginning in early March). Massive sedimentation of phytoplankton is more likely where zooplankton secondary production is uncoupled (e.g. higher latitudinal environments) due to winter diapausal communities not able to respond in time to the increased primary productivity. Zooplankton grazing is an important factor that regulates phytoplankton biomass. Dagg and Ortner (1992) measured the grazing pressure of mesozooplankton in the plume region and the hypoxic region and suggested an immediate initial fate of enhanced primary productivity was to be grazed by the mesozooplankton community.

REFERENCES

ABOU DEBS, C. 1984. Carbon and nitrogen budget of calanoid copepod *Temora stylifera*: effect of concentration and composition of food. Mar. Ecol. Prog. Ser. **15**: 213-223.

ALLDREDGE, A. L., AND C. C. GOTSCHALK. 1989. Direct observations of mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep-Sea Res. **32**: 159-171.

_____, AND _____. 1990. The relative contribution of marine snow of different origins to biological processes in coastal waters. Cont. Shelf Res. **10**: 41-58.

ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems. p. 475-516. *In* M. J. R. Fasham [ed.], Flow of energy and material in marine ecosystems. NATO Conference Series V. Marine Science 13. Plenum.

AYUKAI, T., AND H. HATTORI. 1992. Production and downward flux of zooplankton fecal pellets in the anticyclonic gyre off Shikoku, Japan. Oceanologica Acta **15**: 163-172.

BATHMANN, U. V., AND G. LIEBEZEIT. 1986. Chlorophyll in copepod faecal pellets: change in pellet numbers and pigment content during a declining Baltic spring bloom. Mar. Ecol. **7**: 59-73.

_____, T. T. NOJI, M. VOSS, AND R. PEINERT. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar. Ecol. Prog. Ser. **38**: 45-51.

_____, R. PEINERT, T. T. NOJI, AND B. VON BODUNGEN. 1990. Pelagic origin and fate of sedimenting particles in the Norwegian Sea. Prog. Oceanogr. **24**: 117-125.

_____, T. T. NOJI, AND B. VON BODUNGEN. 1991. Sedimentation of pteropods in the Norwegian Sea in autumn. Deep-Sea Res. **38**: 1341-1360.

BIENFANG, P. K. 1980. Herbivore diet affects fecal pellet settling. Can. J. Fish. Aquat. Sci. **37**: 1352-1357.

BISHOP, J. K., J. M. EDMOND, D. R. KETTEN, M. P. BACON, AND W. B. SILKER. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. **23**: 511-548.

_____, R. W. COLLIER, D. R. KETTEN, AND J. M. EDMOND. 1980 The chemistry, biology and vertical flux of particulate matter from the upper 1500 m of Panama Basin. Deep-Sea Res. **27**: 615-640.

BOCHDANSKY, A. B., AND G. J. HERNDL. 1992. Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. V. Role of fecal pellets in marine snow. Mar. Ecol. Prog. Ser. **89**: 297-303.

BRULAND, K. W., AND M. W. SILVER. 1981. Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). Mar. Biol. **63**: 295-300.

CHIN-LEO, G., AND R. BENNER. 1992. Enhanced bacterioplankton production and respiration at intermediate salinities in the Mississippi River plume. Mar. Ecol. Prog. Ser. **87**: 87-103.

CROUT, R. L. 1983. Wind-driven, near bottom currents over the west Louisiana inner continental shelf. Ph.D. Dissertation, Louisiana State University, Baton Rouge.

DAGG, M. J. 1988. Physical and biological responses to the passage of a winter storm in the coastal and inner shelf waters of the northern Gulf of Mexico. Cont. Shelf Res. **8**: 167-178.

_____, AND P. ORTNER. 1992. Mesozooplankton grazing and the fate of carbon in the northern Gulf of Mexico. p. 117-121. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, J. P. B. ORTNER, AND F. AL-YAMANI. 1988. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. Fish. Bull. **86**: 319-330.

_____, AND W. E. WALSER. 1986. The effect of food concentration on fecal pellet size in marine copepods. Limnol. Oceanogr. **31**: 1066-1071.

DEIBEL, D. 1990. Still-water sinking velocity of fecal material from pelagic tunicate *Dolioletta gegenbauri*. Mar. Ecol. Prog. Ser. **62**: 55-60.

DEUSER, W. G., E. H. ROSS, AND R. F. ANDERSON. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. Deep-Sea Res. **28**: 495-505.

DILLING, L., AND A. L. ALLDREDGE. 1993. Can chaetognath fecal pellets contribute significantly to carbon flux? Mar. Ecol. Prog. Ser. **92**: 51-58.

DINNEL, S. P. 1993. Buoyancy and nutrient exchange in the Mississippi River outflow region. *In* S. E. Lohrenz [ed.], Proceedings of the 1993 NECOP Data Workshop. University of Southern Mississippi, Gulf Coast Campus, Long Beach, Mississippi (abstract) .

DORTCH, Q., AND T. E. WHITLEDGE. 1992. Does nitrogen or silicon limit phytoplankton production in the Mississippi River plume and nearby regions? Cont. Shelf Res. **12**: 1293-1300.

_____, D. MILSTED, N. N. RABALAIS, S. E. LOHRENZ, D. G. REDALGE, M. J. DAGG, R. E. TURNER, AND T. E. WHITLEDGE. 1992. Role of silicate availability in phytoplankton species composition and the fate of carbon. p. 76-85. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, N. N. RABALAIS, R. E. TURNER, AND G. T. ROWE. 1994 Respiration rates and hypoxia on the Louisiana Shelf. Estuaries **17**: 862-872.

DUNBAR, R. B., AND W. H. BERGER. 1981. Fecal pellet flux to modern bottom sediment of Santa Barbara Basin (California) based on sediment trapping. Geol. Soc. Am. Bull. **92**: 212-218.

ELDER, D. L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. BMB Publ. **5**: 1-38.

_____, AND S. W. FOWLER. 1977. Polychlorinated biphenyls: Penetration into deep ocean by zooplankton fecal pellet transport. Science **197**: 459-461.

FOWLER, S. W. 1977. Trace elements in zooplankton particulate products. Nature **269**: 51-53.

_____, S. BALLESTRA, J. LA. ROSA, AND R. FUKAI. 1983. Vertical transport of particulate-associated plutonium and americium in the northeast Pacific. Deep-Sea Res. **30**: 1221-1233.

_____, L. F. SMALL, AND J. LA ROSA. 1991. Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter. Oceanologia Acta **14**: 77-85.

FUKUCHI, M., H. SAKASI, H. HATTORI, O. MATSUDA, A. TANIMURA, N. HANDA, AND C. P. MCROY. 1993. Temporal variability of particulate flux in the northern Bering Sea. Cont. Shelf Res. **13**: 693-704.

GARDNER, W. D. 1989. Baltimore Canyon as a modern conduit of sediment to the deep sea. Deep-Sea Res. **36**: 323-358.

HONJO, S. 1977. Biogenic carbonate particles in the ocean: Do they dissolve in the water column? p. 269-294. *In*. N. R. Andersen and A. A. Malahoff [eds.], The fate of fossil fuel CO_2. Plenum.

_____. 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. Mar. Res. **38**: 53-97.

_____. 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science **218**: 883-884.

_____, AND M. R. ROMAN. 1978. Marine copepod fecal pellets: production, preservation and sedimentation. J. Mar. Res. **36**: 45-57.

ISEKI, K. 1981. Particulate organic matter transport to the deep-sea by salp fecal pellets. Mar. Ecol. Prog. Ser. **5**: 55-60.

JOHANNES, R. E., AND M. SATOMI. 1966. Composition and nutritive value of fecal pellets of a marine crustacean. Limnol. Oceanogr. **11**: 191-197.

JUMARS, P. A., D. PENRY, J. A. BAROSS, M. J. PERRY, AND B. FROST. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res. **36**: 483-495.

JUSTIC', D., N. N. RABALAIS, R. E. TURNER, AND W. J. WISEMAN JR. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. Mar. Pollut. Bull. **26**: 184-189.

_____, _____, AND _____. (in press a). Riverborne nutrients, hypoxia and coastal ecosystem evolution: Biological responses to long-term changes in nutrient loads carried by the Po and Mississippi Rivers. *In* K. Dyer [ed.], Changes in fluxes in estuaries: Implications from science to management. Proceedings, ECSA22 Symposium, Joint ESCA/ERF Conference, International Symposium Series, Olsen & Olsen.

_____, _____, AND _____. (in press b). Stoichiometric nutrient balances and origin of coastal eutrophication. Mar. Pollut. Bull.

KARL, D. M., AND G. A. KNAUER. 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence for multiple zones of biological activity. Deep-Sea Res. **31**: 221-243.

_____, _____, J. H. MARTIN, AND B. B. WARD. 1984. Bacterial chemolithotrophy in association with sinking particles. Nature **309**: 54-56.

KNAUER, G. A., AND J. H. MARTIN. 1981. Primary production and carbon-nitrogen fluxes in the upper 1500 m of the northeast Pacific. Limnol. Oceanogr. **26**: 97-108.

_____, _____, AND K. W. BRULAND. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res. **26**: 97-108.

LAMPITT, R. S., T. NOJI, AND R. VON BONUNGEN. 1990. What happens to zooplankton faecal pellets? Implications for material flux. Mar. Biol. **104**: 15-23.

LAWS, E. A., P. K. BIENFANG, D. A. ZIEMANN, AND L. D. CONQUEST. 1988. Phytoplankton population dynamics and the fate of production during the spring bloom in Auke Bay, Alaska. Limnol. Oceanogr. **33**: 57-65.

LOHMANN, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeeratftriebs. Arch. Protistenka **1**: 89-165.

LOHRENZ, S. E., M. J. DAGG, AND T. E. WHITLEDGE. 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Cont. Shelf Res. **10**: 639-664.

_____, G. L. FAHNENSTIEL, AND D. G. REDALGE. 1994. Spatial and temporal variations of photosynthetic parameters in relation to environmental conditions in northern Gulf of Mexico coastal waters. Estuaries **17**: in press.

LONGHURST, A. G., AND W. G. HARRISON. 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. **35**: 881-889.

MACEINA, M. J., P. W. BETTOLI, AND D. R. DEVRIES. 1994. Use of a split-plot analysis of variance design for repeated-measure fishery data. Fisheries **19**: 14-20.

MADIN, L. P. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar. Biol. **67**: 39-45.

MAITA, Y., T. ODATE, AND M. YANADA. 1988. Vertical transport of organic carbon by sinking particles and the role of zoo- and phytogenic matters in neritic waters. Bull. Fac. Fish. Hokkaido Univ. **39**: 265-274.

MARTIN, J. H., AND G. A. KNAUER. 1982. Manganese cycling in northeast Pacific equatorial waters. J. Mar. Res. **40**: 1212-1225.

_____, _____, D. M. KARL, AND W. W. BROENKOW. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res. **34**: 267-285.

MATSUEDA, H., N. HANDA, I. INOUE, AND H. TAKANO. 1986. Ecological significance of salp fecal pellets collected by sediment traps in the eastern North Pacific. Mar. Biol. **91**: 421-431.

MIQUEL, J. C., S. W. FOWLER, J. LA. ROSA, AND P. BAUT-MENARD. 1994. Dynamics of downward flux of particles and carbon in the open northwestern Mediterranean Sea. Deep-Sea Res. **41**: 243-265.

MULLER, R. A. 1977. A synoptic climatology for environmental baseline analysis: New Orleans. J. Appl. Metero. **16**: 20-33.

MULLIN, M. M., R. B. SLOAN, AND R. W. EPPLEY. 1966. Relationship between carbon content, cell volume, and area in phytoplankton. Limnol. Oceanogr. **11**: 307-311.

NOJI, T. T. 1991. The influence of macrozooplankton on vertical particulate flux. Sarsia **76**: 1-9.

PAFFENHOFER, G. A., AND S.C. KNOWLES. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. J. Mar. Res. **37**: 35-49.

PEINERT, R., B. VON BODUNGEN, AND V. S. SMETACEK. 1989. Food web structure and loss rate. p. 35-48. *In*: W. H. Berger, V. S. Smetacek and G. Wefer [eds.], Productivity of the ocean: Present and past. Wiley & Sons.

PILSKALN, C. H., AND S. HONJO. 1987. The fecal pellet fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles **1**: 31-48.

PRAHL, F. G., AND R. CARPENTER. 1979. The role of zooplankton fecal pellets in the sedimentation of polycyclic aromatic hydrocarbons in Dabob Bay, Washington. Geochim. Cosmochim. Acta **43**: 1959-1972.

PRIOR, D. G., B. D. BORNHOLD, W. J. WISEMAN, JR., AND D. R. LOWE. 1987. Turbidity current activity in a British Columbia fjord. Science **237**: 1330-1333.

QURESHI, N. A., N. N. RABALAIS, AND Q. DORTCH. 1992. Seasonal differences in sedimentation of zooplankton fecal pellets in the northern Gulf of Mexico. p. 122-125. *In* Proceedings, NECOP Synthesis Meeting, Publ. NO. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. p. 35-47. *In* R. V. Tyson, and T. H. Pearson [eds.], Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, The Geological Society, London.

_____, _____, AND _____. 1992. Distribution and characteristics of hypoxia on the Louisiana shelf in 1990 and 1991. p. 15-20. *In*: Proceedings, NECOP Synthesis Meeting, Publ. NO. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, L . E. SMITH, E. B. OVERTON, AND A. L. ZOELLER. 1993. Influence of hypoxia on the interpretation of effects of petroleum production activities. OCS Study/MMS 93-0022. U. S. Dept. of Interior, Mineral Management Service, Gulf of Mexico OCS Region, New Orlean, Louisiana, 158 p.

_____, _____, AND _____. 1994a. Hypoxia conditions in bottom waters on the Louisiana-Texas shelf. p 50-54. *In* M. J. Dowgiallo [ed.], Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding, Special NOAA Report, National Oceanic and Atmospheric Administration, Coastal Ocean Office, Silver Spring, Maryland.

_____, W. J. WISEMAN, JR., AND R. E. TURNER. 1994b. Comparison of continuous records of near bottom dissolved oxygen from the hypoxic zone of Louisiana. Estuaries **17**: 850-861.

_____, R. E. TURNER, D. JUSTIC', Q. DORTCH ,W. J. WISEMAN, JR., AND B. K. SEN GUPTA. (submitted). Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. Estuaries.

RIEBESELL, U. 1989. Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom. Mar. Ecol. Prog. Ser. **54**: 109-119.

ROBERTSON, J. R., K. BANCROFT, G. VERMEER, AND K. PLAISIER. 1980. Experimental studies on the foraging behavior of the sand fiddler crab *Uca pugilator* (Bosc, 1802). J. Exp. Mar. Biol. Ecol. **44**: 67-83.

ROY, S., AND S. A. POULET. 1990. Laboratory study of the chemical composition of aging copepod fecal material. J. Exp. Mar. Biol. Ecol. **135**: 3-18.

SAS INSTITUTE. 1985. SAS User's Guide: Statistics, Version 5 edition. SAS Institute Inc., North Carolina, 956 p.

SASAKI, H., H. HATTORI, AND S. NISHIZAWA. 1988. Downward flux of particulate organic matter and vertical distribution of calanoid copepods in the Oyashio water in summer. Deep-Sea Res. **35**: 505-515.

SCHARADER, H. J. 1971. Fecal pellets: role in sedimentation of pelagic diatoms. Science **174**: 55-57.

SHANKS, A. L., AND J. D. TRENT. 1980. Marine snow: sinking rates and potential role in vertical flux. Deep-Sea Res. **27**: 137-143.

SHUMAN, F. R. 1978. The fate of phytoplankton chlorophyll in the euphotic zone: Washington coastal waters. Ph.D. Dissertation. Washington State University. 238 p.

SILVER, M. W., AND A. L. ALLDREDGE. 1981. Bathypelagic marine snow: deep-sea and detrital community. J. Mar. Res. **39**: 501-530.

SKLAR, F. H., AND R. E. TURNER. 1981. Plankton production in Louisiana coastal zone as influenced by the Mississippi River. Contrib. Mar. Sci. **24**: 93-106.

SMALL, L. F., S. W. FOWLER, AND M. Y. UNLU. 1979. Sinking rates of natural copepod fecal pellets. Mar. Biol. **51**: 233-241.

_____, _____, S. A. MOORE, AND J. LAROSA. 1983. Dissolved and fecal pellet carbon and nitrogen release by zooplankton in tropical waters. Deep-Sea Res. **30**: 1199-1220.

_____, G. A. KNAUER, AND M. D. TUEL. 1987. The role of sinking fecal pellets in stratified euphotic zones. Deep-Sea Res. **34**: 1705-1712.

_____, M. R. LANDRY, R. W. EPPLEY, AND A. F. CARLUCCI. 1989. Role of plankton in the carbon and nitrogen budgets of Santa Monica Basin, California. Mar. Ecol. Prog. Ser. **56**: 57-74.

SMAYDA, T. J. 1969. Some measurements of sinking rates of fecal pellets. Limnol. Oceanogr. **14**: 621-625.

SMETACEK, V. S. 1980. Zooplankton standing stock, copepod fecal pellets and particulate detritus in Kiel Bight. Estuar. Coast. Mar. Sci. **11**: 470-490.

STARESINIC. N., J. FARRINGTON, R. B. GAGOSIAN, C. H. CLIFFORD, AND E. M. HULBURT. 1983. Downward transport of particulate matter in the Peru coastal upwelling: role of anchoveta, *Engraulis ringens*. *In* E. Suess and J. Thiede [eds.], Coastal upwelling. Its sediment record. Part A: responses of the sedimentary regime to present coastal upwelling. Plenum.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw Hill.

STRATHMANN, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. **12**: 411-418.

TURLEY, C. M. 1992. Formation, vertical flux and remineralization of aggregates in the ocean: a short review. Arch. Hydrobiol. Beih. Ergebn. Limnol. **37**: 155-163.

TURNER, J. T. 1979. Microbial attachment to copepod fecal pellets and its possible ecological significance. Trans. Amer. Microsc. Soc. **98**: 131-135.

_____, AND J. G. FERRANTE. 1979. Zooplankton fecal pellets in aquatic ecosystems. BioScience **29**: 670-675.

TURNER, R. E., AND R. A. ALLEN. 1982. Plankton respiration in the bottom waters of the Mississippi River Delta Bight. Contrib. Mar. Sci. **25**: 173-179.

_____, AND N. N. RABALAIS. 1991. Changes in Mississippi River water quality this century and implications for coastal food webs. BioScience **41**: 140-147.

_____, AND _____. 1994. Coastal eutrophication near the Mississippi river delta. Nature **368**: 619-621.

_____, AND _____. (in press). Changes in silicate-based primary production influenced by the Mississippi River outflow. *In* K Dyer [ed.], Changes in fluxes in estuaries: Implications from science to management. Proceedings Joint ECSA/ERF Conference, Olsen and Olsen, International Symposium Series.

URBAN, J. L. 1992. Seasonal changes in the chemical and physical characterstics of *Calanus finmarchicus* and *Oikopleura vanhoeffeni* fecal pellets. M.S. Thesis. Memorial Univ., Newfoundland, 150 p.

_____, C. H. MCKENZIE, AND D. DEIBEL. 1992. Seasonal differences in the content of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets: illustrations of zooplankton food web shifts in coastal Newfoundland waters. Mar. Ecol. Prog. Ser. **84**: 255-264.

URRERE, M. A., AND G. A. KNAUER. 1981. Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. J. Plankton Res. **3**: 369-387.

VOSS, M. 1991. Content of copepod faecal pellets in relation to food supply in Kiel Bight and its effect on sedimentation rate. Mar. Ecol. Prog. Ser. **75**: 217-225.

WALSH, I., K. FISHER, D. MURRAY, AND J. DYMOND. 1988. Evidence for resuspension of rebound particles from near-bottom sediment traps. Deep-Sea Res. **35**: 59-70.

WASSMANN, P. 1983. Sedimentation of organic and inorganic particulate material in Lindaspollene, a stratified, land-locked fjord in western Norway. Mar. Ecol. Prog. Ser. **13**: 237-248.

WIEBE, P. H., S. H. BOYD, AND C. WINGET. 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean, Bahamas, with a description of a new sedimentation trap. J. Mar. Res. **34**: 341-354.

YOUNGBLUTH, M. J., T. G. BAILEY, P. J. DAVOLL, C. A. JACOBY, P. I. BLADES-ECKELBARGER, AND C. A. GRISWOLD. 1989. Fecal pellet production and diel migratory behavior by the euphausiid *Meganyctiphanes norvegica* affect benthic-pelagic coupling. Deep-Sea Res. **36**: 1491-1501.

CHAPTER 3

THE IMPORTANCE OF FECAL PELLET FLUX OF CARBON TO THE SEA FLOOR ON A RIVER-INFLUENCED CONTINENTAL SHELF

INTRODUCTION

The sedimentation of biologically produced particles out of the photic layer, the mechanisms controlling that flux and the magnitude of the process relative to primary production are of great interest for understanding the carbon cycle in the ocean (Eppley & Peterson 1979, Martin et al. 1987). McCave (1975) suggested that rare larger particles dominate the downward flux of organic carbon in comparison to smaller suspended particles. Recent sediment trap studies at various depths in shallow and deep oceans sites have now clearly demonstrated the importance of rapidly sinking large particles in transport of material to the sea floor (Wiebe et al. 1976, Knauer et al. 1979, Bishop et al. 1980, Honjo 1978, 1980, 1982, Shanks & Trent 1980, Knauer & Martin 1981, Silver & Alldredge 1981, Martin & Knauer 1982, Betzer et al. 1984). These larger particles are generally composed of zooplankton fecal pellets, zooplankton carcasses and exuviae, phytoplankton remains, and macroscopic aggregates or 'marine snow' (Bishop et al. 1977, Honjo 1978, 1980, Knauer et al. 1979, Shanks & Trent 1980, Urrere & Knauer 1981, Silver & Alldredge 1981, Alldredge & Gotschalk 1989, Riebesell 1989).

It is well recognized that productivity in the euphotic zone regulates the vertical flux of biogenic as well as abiogenic particles in the ocean (Deuser et al. 1981). Sediment trap data have been used to demonstrate a positive correlation between the flux of particulate material and surface primary production for long term data averaged over the year from different oceanographic regions (Suess 1980) and also for short term data from the same oceanographic region with seasonal variations (Deuser & Ross

1980, Betzer et al. 1984). Various investigations of shallow coastal areas have indicated that there is no single mechanism responsible for the transport of particulate organic carbon to sediments. Sinking phytoplankton cells and phytodetritus accounted for nearly two-thirds of the organic carbon flux in Kiel Bight (Baltic Sea) (Smetacek 1980), and uncoupling of primary production from zooplankton grazing resulted in direct sedimentation of spring phytoplankton blooms in the coastal area of a Norwegian fjord (Skjoldal & Wassmann 1986). Hargrave and Taguchi (1978) found seasonal variations in the nature of material sedimented to the bottom whereby zooplankton fecal pellets contributed a larger amount of carbon during summer when the water column was highly stratified, but phytoplankton cells composed a much greater contribution when the water column was mixed in winter. Copepod fecal pellets have been identified as a major contributor to transport of particulate organic carbon to the deeper oceans (Lohmann 1902, Turner & Ferrante 1979, Dunbar & Berger 1981, Urrere & Knauer 1981, Fowler et al. 1983) and shallow coastal areas (Burns et al. 1985, Bochdansky & Herndl 1992).

Various studies using sediment traps to determine flux at different depths have measured numerical and mass fluxes of zooplankton fecal pellets and showed that fecal pellet flux varies as a function of seasonal surface productivity, nutrient levels and water depth (Wiebe et al. 1976, Bishop et al. 1980, Honjo 1978, 1980, Knauer & Martin 1981, Dunbar & Berger 1981, Urrere & Knauer 1981). The zooplankton fecal pellet flux in the open ocean varies 1-10% of the total measured mass flux of particulate organic material below 1000 m (Pilskaln & Honjo 1987). Pelagic food-web interactions such as microbial degradation, coprophagy (reingestion of fecal pellets by zooplankton), coprorhexy (mechanical breakage of fecal material by organisms) and coprochally (loosening of fecal pellets) may result in recycling and remineralization of fecal pellets produced in the photic zone and therefore decrease the flux of fecal pellet carbon (Honjo & Roman 1978, Paffenhofer & Knowles 1979, Lampitt et al. 1990, Noji

1991). Flux of fecal pellet carbon can also be affected by rapid DOC diffusion (as great as 90%) that further promotes pelagic microbial recycling of material in the water column (Jumars et al. 1989). Pilskaln and Honjo (1987) estimated that zooplankton fecal pellets can provide up to 66% of the benthic community carbon requirement. The percent contribution of fecal pellets to flux of particulate organic carbon (POC) varies irregularly with depth. Urrere and Knauer (1981) found an increase of 11 to 19% of fecal pellet flux with an increase in depth from 35 to 150 m.

The export of carbon from surface waters to the lower water column and sediments is particularly interesting on the southeastern Louisiana shelf where the oxidation of fluxed organic material from surface layers leads to oxygen deficiency in the bottom waters. The continental shelf adjacent to the outflows of the Mississippi-Atchafalaya River system is an extremely productive coastal system. Fresh water discharge, much of which is retained on the inner to mid shelf by prevailing winds and large-scale circulation patterns, maintains a stratified system for much of the year, especially in summer. Nutrients delivered in the effluents support elevated primary production in the immediate (329 g C m^{-2} yr^{-1}) and extended plume (290 g C m^{-2} yr^{-1}) regions of the Louisiana inner shelf (Lohrenz et al. 1990, Sklar & Turner 1981). Consequently, the flux of organic material to the seabed is expected to be high. The relative contribution of phytoplankton cells, fecal pellets, detritus, and aggregates to organic flux will likely vary by season and distance from the river effluent in response to nutrient levels and primary production. Particulate organic flux to the seabed in this region is linked to the presence of oxygen-depleted bottom waters (Turner et al. 1987). The timing, amount and organic content of fluxed materials to the lower water column and seabed will likely influence the extent and severity of oxygen depletion.

Oxygen-depleted bottom waters are dominant features of the Louisiana continental shelf especially in summer. The areal extent of hypoxic bottom water

(< 2 mg O_2 l^{-1} dissolved oxygen) covers up to 16,500 km^2, from the Mississippi River delta to the upper Texas shelf, with inter-annual variation (Rabalais et al. 1991, 1992, 1994a). Seasonal and spatial variability in the distribution of hypoxia is related in part to amplitude and timing of Mississippi River discharge. The bottom water hypoxia is more severe and pronounced from mid-May to mid-September when the density difference is greatest between surface and bottom (Rabalais et al. 1994b). Surface water net production lags one month after peak river flow and bottom oxygen deficiency lags two months after peak river flow (Justic' et al. 1993). Strong cross correlations between these factors indicates a close coupling between riverborne nutrients, net productivity and hypoxia (Justic' et al. 1993).

The nature of organic material flux and the relative contribution to the flux by fecal pellets and/or phytoplankton cells has not been examined for the northern Gulf of Mexico on the continental shelf influenced by the Mississippi River. The seasonal variability in nutrient loading, hydrography and phytoplankton community composition are potentially important factors driving variations in the quality and quantity of organic loading to bottom waters on this shelf. These complex interactions may ultimately affect the overall trophic structure and fate of carbon on the shelf.

OBJECTIVES

The objective of this study was to examine the importance of fecal pellet carbon flux in the overall export of particulate matter from surface waters to the seabed on the Mississippi River influenced continental shelf within the zone of seasonally severe hypoxia. I determined differences in particulate matter flux, including total particulate, particulate organic carbon and particulate organic nitrogen, as well as fecal pellet carbon flux (Chapter 2). I compared fecal pellet carbon flux to estimates of phytoplankton carbon flux and determined their relative importance to total carbon

export from the surface waters and their potential to support oxygen deficiency. I tested the following hypotheses:

- fecal pellet carbon flux constitutes the primary source of fluxed carbon,
- fecal pellet carbon flux exceeds phytoplankton carbon flux,
- the dominance of fecal pellet carbon flux is greater in summer than spring, and
- the oxidation of carbon in fluxed fecal pellets is sufficient to induce hypoxia in spring, which is then sustained through the summer by the physical structure of a stratified and stable water column.

I also estimated the percentage of surface water primary production that was exported via fecal pellets or phytoplankton cells by comparing flux data to historical primary production data.

METHODS

Field Collections

Sediment trap samples were collected from a permanent mooring deployed at station C6B in 20 m water depth, located at 28°50.41' N and 90°26.03' W off Terrebonne Bay on the southeastern Louisiana coast. The details of the sediment trap array are given in Chapter 2. Samples were collected from April 17 through December 7, 1991 and from March 2 through October 27, 1992. Ancillary hydrographic data, including temperature, salinity, density and dissolved oxygen, were recorded with a Hydrolab Surveyor 3 or Seabird CTD unit during each collection. Biological data included water column pigments (chlorophyll *a* and phaeopigments) and nutrients collected at the surface, above (6.5 m) and below (14 m) the pycnocline and at the bottom (~ 19 m). Depths of mid-water collections corresponded to the depths of the openings of the sediment traps.

Sediment Trap Processing

Each trap sample was split in a Folsom plankton splitter to dilute materials to appropriate quantities for the various analyses. Eight replicate splits (aliquots) were used for CHN (carbon, hydrogen and nitrogen) analyses and calculations of total particulate material (TPM) and organic carbon and nitrogen. A various number of splits (aliquots) and replicates was used for chlorophyll *a* and phaeopigment determinations.

The subsample for CHN analysis was processed immediately after retrieval of the sample or was frozen and then split further at the time of analysis. The subsample was eventually split to give four replicates that were not acidified and four equal replicates that were acidified to remove carbonate (10% HCl until all fizzing stopped). The splits were filtered onto precombusted (360 °C, 5 h) GF/F filters. Filters were either frozen at -60 °C and then dried at the time of CHN analysis, or dried immediately at 50-60 °C for 10-12 h, and were then analyzed. When dried, filters were pre- and post-weighed for estimation of total particulate material (not acidified, TPM). Filters were packed in nickel sleeves (precombusted at 875 °C for one hour) and were analyzed on a Control Equipment Elemental Analyzer, model 240XA, with a multi-sampler injector for the particulate organic carbon (acidified, POC), and total organic nitrogen (acidified, PON).

The replicate splits were of three kinds: (1) archived frozen liquid sample, split, filtered and analyzed (CHN analysis) later (2) liquid subsample filtered immediately and filters archived frozen for later analysis, and (3) liquid subsample filtered processed, and analyzed immediately. Replicates of each type of treatment were analyzed for significant differences in all sample treatments measured using a single factor ANOVA. No significant differences were found between the processing treatments used.

Sediment Trap Fluxes

Total Particulate Material, Particulate Organic Carbon and Particulate Organic Nitrogen

Mean fluxes X (mg m^{-2} d^{-1}) (n = 4 replicate splits or aliquots) for each trap depth (5-6 m = top and 15 m = bottom) were determined by back calculating the amount of material *X* (mg) in the split (weight of particulate material in case of TPM, POC, and PON analyzed) from the measured amount *x* (mg):

$$X\,(\text{mg}) = x * 2^{(n-1)} \qquad \text{Equation 3.1}$$

where n is the number of splits used to generate replicates.

$$X \text{ flux } (\text{mg } m^{-2}\ d^{-1}) = X\,(\text{mg})/(\text{area of trap mouth} * \text{duration of deployment}) \qquad \text{Equation 3.2}$$

The %TOC (weight percent of total organic carbon) was calculated from carbon determinations on acidified filters of known weight particulate matter. C:N ratios were determined from analysis of particulate carbon and particulate nitrogen on acidified filters.

Chlorophyll *a* and Phaeopigment

One of the sediment trap subsamples was used for estimating total pigment flux (sum of chlorophyll *a* and phaeopigment). Two or three replicates of sediment trap material were filtered onto GF/F filters. The individual filters were placed into 5 ml of a 60:40 DMSO:90% acetone and water solution and extracted in the dark for one hour. Filters were removed and the samples were centrifuged. The fluorescence of the supernatant was recorded before and after acidification (10% HCl) on a Turner Design Model 10 fluorometer. The flux for each trap depth was calculated using a method modified from water column pigment calculations for chlorophyll *a* and phaeopigment.

When more than one filter was used, the fluorescences were summed as indicated below:

Chlorophyll *a* (mg) = {Σ [K (Fo - Fa) * volume extracted]}/1000 Equation 3.3

Phaeopigment (mg) = {Σ [K (AR * Fa - Fo) * volume extracted]}/1000 Equation 3.4

where Fo and Fa are fluorometer readings before and after acidification, and K and AR are calibration constants for the fluorometer. Total pigment flux (mg m^{-2} d^{-1}) was calculated by adding chlorophyll *a* and phaeopigment fluxes, where flux (F) for chlorophyll *a* and phaeopigment was calculated separately as:

F (mg m^{-2} d^{-1}) = Chl *a* (mg) * $2^{(n-1)}$/(area of trap mouth * duration of deployment) Equation 3.5

F (mg m^{-2} d^{-1}) = Phaeo (mg) * $2^{(n-1)}$/(area of trap mouth * duration of deployment) Equation 3.6

Chlorophyll *a* may be degraded and transformed into phaeopigments in the sediment traps during the longer deployments. However, Peterson et al. (1993) observed no significant differences between chlorophyll *a*, phaeophorbides, and total pigment in treated (mercuric chloride, formalin, and brine) and untreated traps. Because the sediment traps were treated with glutaraldehyde and the effect of glutaraldehyde was not known, I did not focus on either chlorophyll *a* and phaeopigment fluxes but summed them to obtain total pigment flux which is referred to below as 'pigment'.

Fecal Pellet Carbon Flux

Fecal pellet carbon flux was calculated from data on average fecal pellet volume and a conversion to carbon as described in Chapter 2.

Phytoplankton Carbon (P_{cell}) Flux

One archived trap subsample was used to calculate the phytoplankton carbon flux for 1991 (Q. Dortch unpubl.). Phytoplankton cells were counted, measured and converted to phytoplankton carbon flux (P_{cell}) using a carbon to cell volume relationship. Q. Dortch (pers. comm.) employed a simple linear regression on cell size (cell volume) and carbon content based on literature values of carbon to cell volume ratios to calculate a factor of 0.185 pg C μm^{-3} to estimate phytoplankton carbon flux.

Statistical Analyses

A univariate split-plot design ANOVA, where class variables are assigned to subunits, was used to analyze the variability of sediment trap data between years, seasons and depths. A greater amount of information can be obtained when class variables are assigned to subunits (Steel & Torrie 1980). A repeated measure ANOVA or split-plot design was also appropriate to use in this case as samples were collected at a fixed station over time, which violated the first assumption of random sampling of ANOVA. A repeated measure ANOVA or split plot design has been employed for ecological experiments where data were repeatedly collected from the same organism and for fisheries data collected at fixed stations over time (Maceina et al. 1994). This technique partitions the variation due to fixed sampling site, treatments or manipulations, correlation that may occur over time, and interactions among class variables. Partitioning increases accuracy and provides new insights on different responses of the variables.

The split-plot design was divided into a main plot which included year, season and year*season interactions. Replication was sought from different dates by partitioning sample dates into seasons, spring, summer and fall (Appendix B). This division was based on the hydrography and vertical structure of water column rather than the calendar year. The summer period was distinguished from spring and fall by

having a relatively stable water column, a strong pycnocline (around 8 to 15 m) (Figs. 2.1 and 2.2) that separated a low dissolved oxygen bottom layer from oxygen saturated surface waters, and negligible bottom water currents (2-3 cm s^{-1}) (W. J. Wiseman, Jr., unpubl. data). Depth (5-6 m = top trap, 15 m = bottom trap) and its interactions were tested in the subplot.

Tukey's studentized range test, a pair-wise comparison, was employed to specify interannual, seasonal, and depth related variability, because it is more conservative than other tests and has a family-wise error rate.

The assumptions for normally distributed data and homogeneity of variance were tested by univariate analysis and plotting residuals. Data were transformed to $\log_{10}$ values to stabilize variances for the analyses, when data were not normally distributed (Shapiro-Wilk statistics, $Pr < W = 0.0001$) and the mean values were proportional to their variances. Type III sum of squares were used to compute mean square errors, because of the unbalanced data (Steel & Torrie 1980).

The sediment trap flux data were correlated to identify relationships between the different components. The same data were also correlated with environmental data, including water temperature and salinity, total pigments, delta sigma t (difference between surface and bottom, a measure of the strength of the pycnocline) and surface water salinity lagged one month. The upper water column (U) was an average of surface water and 6.5 m depth, and the lower water column (L) was an average for 14 m depth and bottom. The best fit model was developed from the environmental variables using a stepwise multiple regression model with forward selection.

All statistical analyses were done using PC SAS version 6.04 (SAS Institute 1985).

Resuspension Potential of Sediments

I examined the potential of bottom currents to resuspend sediments by determining the critical bed shear stress from Shield's entrainment function for a range of silt-sized particles (Appendix A). I calculated critical velocity (U*) at 1 m above the seabed. A limited current meter record from 1 m above the bed (Endeco model 174) was obtained for May 10 to August 24, 1992 (W. J. Wiseman, Jr. unpubl. data). Other records from the bottom current meter in 1991 and 1992 deployments were not reliable (W. J. Wiseman, Jr. pers. comm.).

RESULTS

Water Column Characteristics

A stratified system dominated most of both years. The density distribution was controlled primarily by salinity (Figs. 2.1 and 2.2). The water column was mostly isothermal in spring and fall of both years; however, solar heating of the upper water column contributed to the development of a thermocline and an increased density gradient in summer. Dissolved oxygen concentrations were low (< 2 mg O_2 l^{-1}) from June through the end of August (days 177-237) in 1991 and from late May through late August (days 149-237) in 1992 (Figs. 2.1-2.4). The periods of hypoxia coincided with greater surface-to-bottom differences in density. The stable, stratified water column was disrupted by a series of frontal passages in fall 1991 and the passage of Hurricane Andrew on August 25, 1992 and subsequent cold fronts. The water column remained well mixed through the fall of 1991, but a stratified system reestablished in fall of 1992.

Nitrate concentrations were high in surface waters in spring of both years (Figs. 2.5 and 2.6). High nitrate concentrations were also evident in bottom waters in spring and occasionally in summer. The concentrations of silicate, phosphate and ammonia were elevated in surface waters in spring 1991, but were not as high in 1992. Nitrite

concentrations were higher in bottom waters in summer of both years, with small peaks in surface as well as bottom waters in fall. Bottom water silicate, phosphate and ammonia concentrations were usually higher in the summer in both years.

Chlorophyll *a* concentrations were high in surface waters in late spring (April-May) of both years (Figs. 2.7 and 2.8). Very high chlorophyll *a* concentrations were seen in bottom waters in summer 1992. Chlorophyll *a* concentrations were more moderate throughout the water column in summer and fall of 1991. Phaeopigment concentrations were high in the upper water column in spring and fall of 1991 and fall 1992, and high in bottom waters of summer 1992.

Sediment Trap Fluxes

Total Particulate Material - The total particulate material flux (TPM) ranged from $1.5*10^3$ to $1.4*10^5$ and from $3.3*10^3$ to $2.0*10^5$ mg m^{-2} d^{-1} for the top and bottom traps, respectively (Fig. 3.1, Appendix B). The average TPM flux was higher into the bottom trap in both years (Fig. 3.1, Tables 3.1 and 3.2). The TPM flux into the top trap in spring and summer of 1991 was higher than the average for fall, but these differences were not significant (Appendix B, Table 3.1). The high TPM flux into the top trap on June 17, 1992 (Fig. 3.1) was influenced by an abundance of pteropods. Pteropods were also present in the top trap samples for June 6 and July 6, but did not substantially increase the TPM flux above the summer average. The TPM flux was significantly different between years and seasons, with a significant year*season interaction (Table 3.1). The TPM flux average for both traps was higher in 1991 than in 1992. The fall fluxes were much higher than either the spring or the summer fluxes (Table 3.2).

Particulate Organic Carbon - The total organic carbon (POC) flux ranged from $1.2*10^2$ to $7.0*10^4$ and from $6.8*10^1$ to $1.8*10^3$ mg C m^{-2} d^{-1} for the top and bottom traps, respectively (Fig. 3.1, Appendix B). The average POC flux was higher into the

Table 3.1. Split-plot analysis of variance results for sediment trap fluxes, constituents and ratios for station C6B during 1991 and 1992.

Variables	df	TPM** P>F	POC P>F	PON** P>F	Pigment** P>F	TOC** P>F	C:N P>F	FPC:POC P>F
Pr < W	52	0.8555	0.1871	0.9763	0.8906	0.8764	0.0874	0.9766
Model	33	0.0005*	0.2726	0.3174	0.0005*	0.0001*	0.0001*	0.4865
Main Plot***								
Year	1	0.0060*	0.0771	0.4397	0.4165	0.0051*	0.0071*	0.9217
Season	2	0.0001*	0.1431	0.0519*	0.0007*	0.0002*	0.0001*	0.0097*
Year*Season	2	0.0001*	0.0043*	0.0003*	0.0012*	0.6768	0.3166	0.0337*
Date (Year*Season)	22	0.4174	0.7718	0.8982	0.0781	0.3123	0.0025*	0.7671
Sub-plot								
Depth	1	0.0145*	0.0231*	0.0052*	0.0392*	0.0001*	0.0001*	0.1341
Year*Depth	1	0.1677	0.3363	0.7586	0.3217	0.0969	0.1251	0.1431
Season*Depth	2	0.4821	0.3145	0.3391	0.0673	0.2893	0.0004*	0.1274
Year*Season*Depth	2	0.6816	0.2482	0.9715	0.0961	0.8381	0.0178*	0.3434

TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
TOC = weight percent of total organic carbon
FPC = fecal pellet carbon flux (from Chapter 2)

* significant at alpha error = 0.05
** log10 transformed data
*** test of hypothesis with error = Date (Year*Season)

Table 3.2. Tukey's studentized range test for sediment trap fluxes, constituents and ratios for station C6B during 1991 and 1992. Means with same letter within each variable are not statistically different at alpha = 0.05.

Variables	Number of Samples	TPM* mg/m^2/d means	POC mg/m^2/d means	PON* mg/m^2/d means	Pigment* mg/m^2/d means	TOC* % means	C:N Ratio means	FPC mg/m^2/d means	FPC:POC % means
Year									
1991	30	54131.0 A	1064.0 A	138.3 A	3.9 A	3.3 B	8.1 A	230.8 A	44.8 A
1992	23	21146.0 B	753.3 A	126.6 A	1.4 B	9.0 A	6.7 B	98.6 A	34.5 A
Season									
Spring	13	38833.0 B	1258.0 A	175.5 A	6.8 A	7.3 A	7.9 B	350.8 A	42.8 A
Summer	24	11360.0 B	611.2 A	106.3 B	0.9 B	7.2 A	6.5 C	42.1 B	28.6 B
Fall	16	83301.0 A	1138.8 A	139.2 A	2.5 B	2.4 B	8.6 A	236.1 AB	56.0 A
Depth									
Top ~5-6 m	27	26441.0 B	1283.4 A	197.1 A	3.0 A	9.3 A	6.9 B	229.8 A	45.7 A
Bottom ~15 m	26	53707.0 A	561.2 B	66.9 B	2.6 B	2.1 B	8.2 A	119.9 A	65.3 A

* analysis was performed on log10 transformed data but means are presented as untransformed data
TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
TOC= weight percent of total organic carbon
FPC = fecal pellet carbon flux (from Chapter 2)

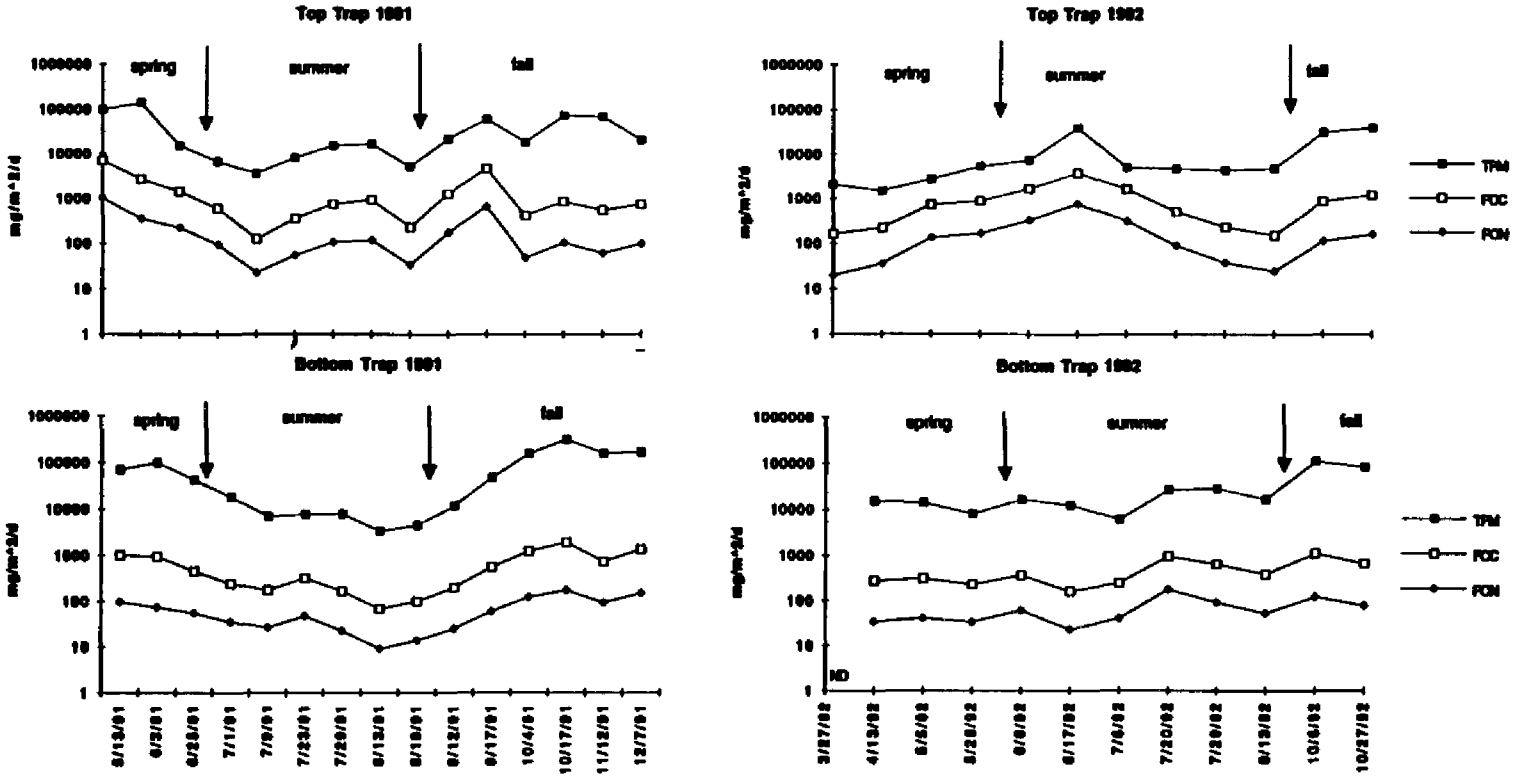


Figure 3.1. Temporal variation of total particulate material (TPM), particulate organic carbon (POC), and particulate organic nitrogen (PON) fluxes (mg $m^{-2} d^{-1}$) collected at 5-6 m (top) and 15 m (bottom) depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

top trap in both years (Fig. 3.1, Tables 3.1 and 3.2). Although the average 1991 POC flux was an order of magnitude greater than the 1992 POC flux, the difference was not statistically significant. Similarly, the average spring POC flux was higher than either fall or summer, but the differences were not statistically significant. The POC flux was highest in the top trap in 1992 for the summer collections on June 6, June 17 and July 6, when pteropods composed a majority of the trap sample.

Particulate Organic Nitrogen - The total organic nitrogen (PON) flux ranged from $1.9*10^1$ to $1.0*10^3$ and from $9.0*10^1$ to $1.7*10^2$ mg N m^{-2} d^{-1} for the top and bottom traps, respectively (Figure 3.1, Appendix B). The average PON flux into the top trap was higher in both years (Fig. 3.1, Tables 3.1 and 3.2). Average PON fluxes were not significantly different between years, but were significantly different between seasons with a significant year*season interaction (Table 3.1). The PON flux was significantly lower in summer than either spring or fall (Table 3.2). The same peak seen in TPM and POC in the June 17 sample was also evident in the PON fluxes.

Total Pigments - The total pigment fluxes were composed primarily of phaeopigments (Figure 3.2, Appendix B). The total pigment fluxes ranged from 0.06 to 36.00 and from 0.20 to 12.99 mg m^{-2} d^{-1} for the top and bottom traps, respectively. Fluxes of total pigments were higher into the top trap than into the bottom trap in both years (Fig. 3.2, Tables 3.1 and 3.2). Average total pigment flux was higher in 1991 than in 1992 (Table 3.2), but the ANOVA model for year differences was not significant (Table 3.1). The total pigment flux was significantly higher in spring than in either summer or fall (Tables 3.1 and 3.2).

Phytoplankton Carbon - Phytoplankton carbon flux (P_{cell}) was estimated for 1991 samples (Q. Dortch unpubl. data). The P_{cell} flux ranged from 1.2 to 250.8 and from 0.9 to 86.0 mg C m^{-2} d^{-1} for the top and bottom traps, respectively (Fig. 3.3, Appendix B). The P_{cell} flux was higher into the top trap than into the bottom trap, but the difference was not statistically significant (single factor ANOVA, $P > F = 0.27$).

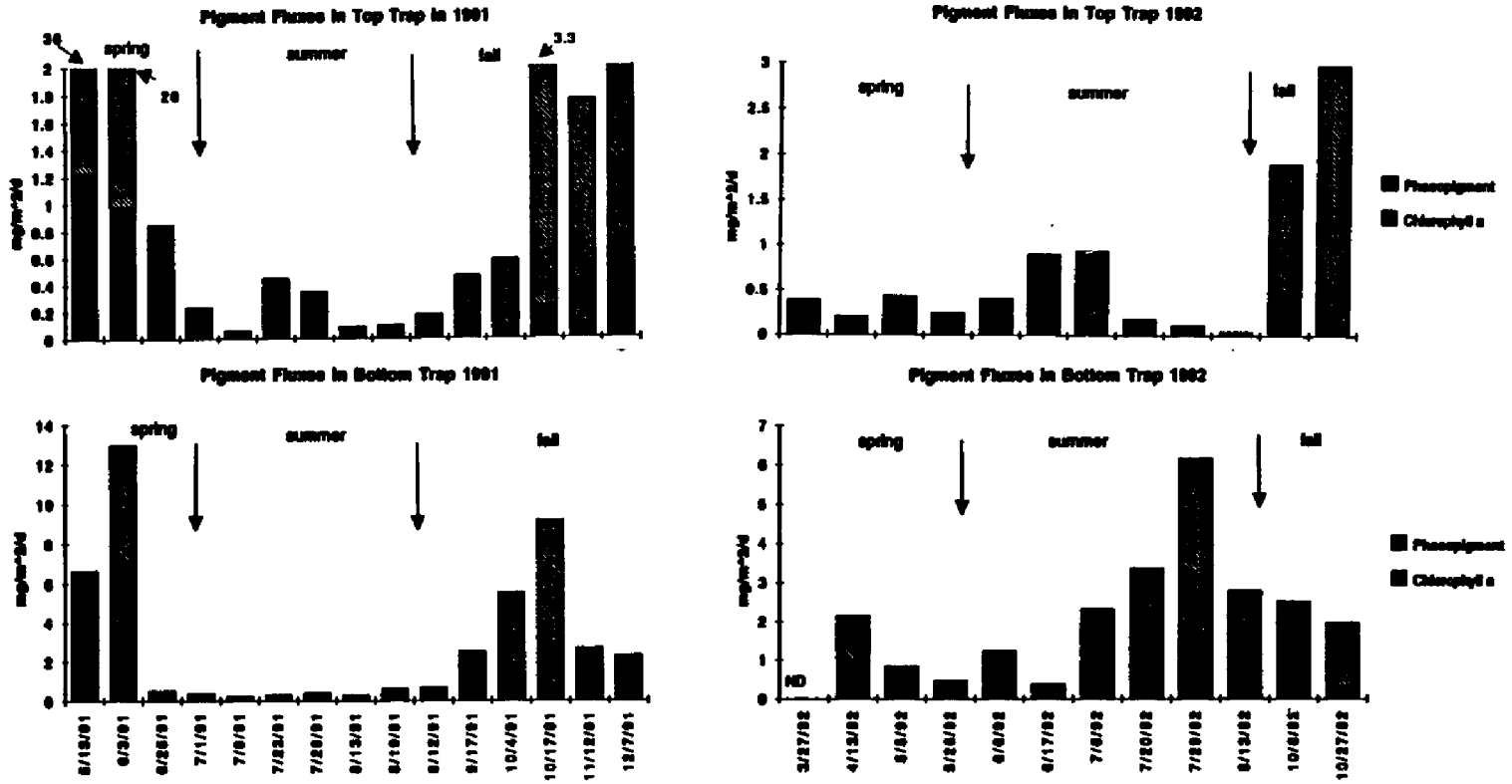


Figure 3.2. Temporal variation in total pigment flux (mg $m^{-2} d^{-1}$): chlorophyll *a* and phaeopigment fluxes are stacked to show the total pigment flux at 5-6 m (top) and 15 m (bottom) depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

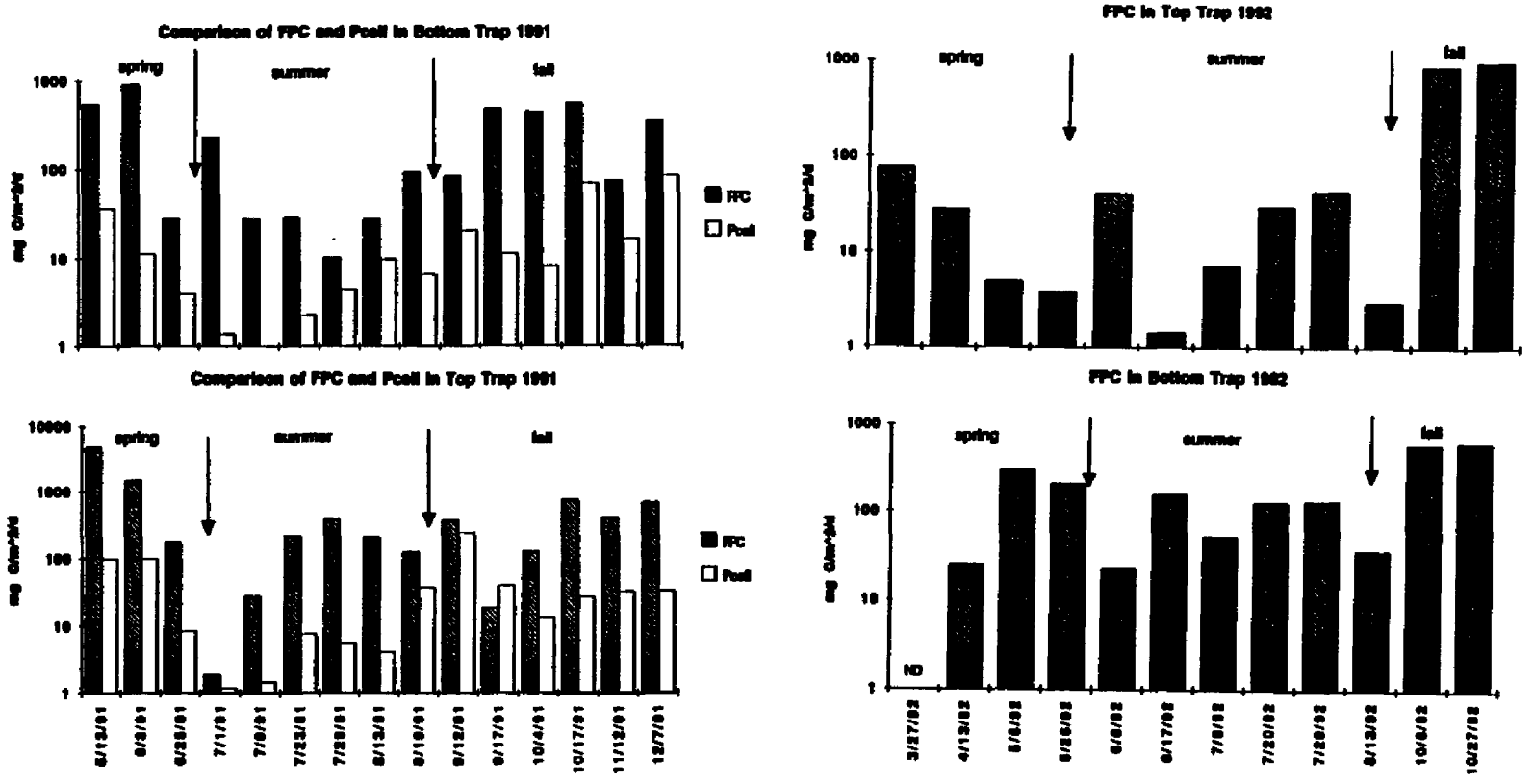


Figure 3.3. Comparison of fecal pellet carbon (FPC, from Chapter 2) and phytoplankton carbon (P_{cell}, 1991 only, Q. Dortch unpubl. data) fluxes (mg m^{-2} d^{-1}) collected at 5-6 m (top) and 15 m depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; ND is no data.

Top trap fluxes were similar between spring and fall, but both were much higher than in summer; bottom trap fluxes were highest in fall, lowest in summer, with spring intermediate. The P_{cell} fluxes (log_{10} transformed) were significantly different between seasons both in the top as well as in the bottom trap ($P > F = 0.015$ and $P > F = 0.011$, respectively).

Comparison of Fecal Pellet Carbon and Phytoplankton Carbon Fluxes

Fecal pellet carbon flux (FPC, described in Chapter 2) into both traps was higher than the P_{cell} flux, except for a single sample date for the bottom trap in September 1991 (Fig. 3.3, Appendix B). The differences between the FPC and P_{cell} fluxes were not statistically significant for the top trap (single factor ANOVA, $P > F = 0.059$), but were for the bottom trap ($P > F = 0.002$). The P_{cell} followed temporal variation of fecal pellet carbon flux with high flux in spring and fall and low flux in the summer (Fig. 3.3). The same seasonal trends were seen in fecal pellet carbon flux and phytoplankton carbon flux -- that is, spring > fall > summer for the top trap and fall > spring > summer for the bottom trap.

Sediment Trap Total Organic Carbon and C:N

The percent total organic carbon (%TOC) ranged from 0.80 to 34.23 and from 0.50 to 4.92 for the top and bottom traps, respectively (Figure 3.4, Appendix B). The %TOC was significantly different between years, seasons and depths (Table 3.1). The %TOC was higher in 1992 than in 1991, was higher in both spring and summer than in fall, and was higher in the top trap than in the bottom trap (Table 3.2).

The C:N ratios ranged from 5.17 to 9.01 and from 6.16 to 13.03 for the top and bottom traps, respectively (Figure 3.4, Appendix B). There was a significant difference in the C:N ratios between years, seasons, and depths (Table 3.1). The C:N ratios were higher in 1991 than in 1992, were higher in the fall than in the spring which

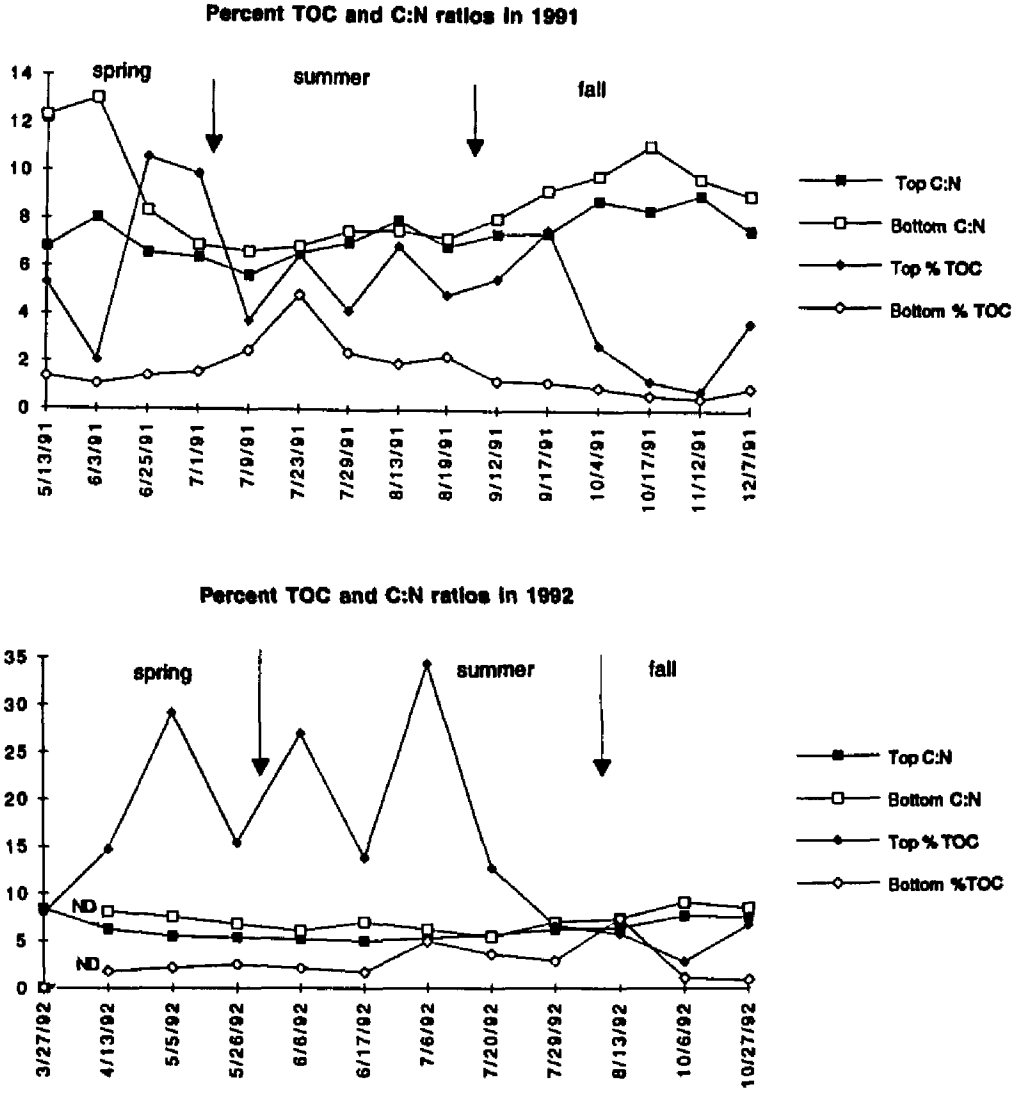


Figure 3.4. Temporal variation in percent total organic carbon (%TOC) and C:N ratios of material collected in sediment traps during 1991 and 1992 at 5-6 m (top) and 15 m (bottom) depths at station C6B. Arrows delineate dates included in each season; ND is no data.

were both higher than the summer, and were higher in the bottom trap than in the top trap (Table 3.2).

Contribution of Fecal Pellet Carbon (FPC) Flux and Phytoplankton Carbon (P_{cell}) Flux to Particulate Organic Carbon (POC) Flux

The contribution of fecal pellet carbon flux (%FPC) to the particulate organic carbon flux (POC) ranged from 0.4 to 99.8% and from 0.3 to 99.9% in the top and bottom traps, respectively (Fig. 3.5, Appendix B). There were major fluctuations between dates and no obvious seasonal trends. The seasonal average for summer across both years, however, was significantly lower than the averages for either spring or fall (Table 3.2). There were no year or depth-related differences in %FPC:POC (Table 3.2)

The $\%P_{cell}$ contribution to POC ranged from 0.2 to 19.8 % and from 0.5 to 14.6 % in the top and bottom traps, respectively (Figure 3.5, Appendix B, 1991 data only). Overall, the $\%P_{cell}$ contribution to POC was lower than the FPC in the top and the bottom trap. There were somewhat higher $\%P_{cell}$ contributions to POC in late summer and early fall in both the top and the bottom traps (Fig. 3.5), but there was no significant difference between seasonal averages for traps ($P > F = 0.56$ and $P > F = 0.70$, respectively, single factor ANOVA). There was no significant difference in $\%P_{cell}$:POC between the top and the bottom trap ($P > F = 0.80$).

Relationships between Sediment Trap Flux Variables

The FPC in to the top trap for 1991 was correlated with top trap TPM, POC, PON and total pigment fluxes and with the bottom trap C:N ratio (Table 3.3). The bottom trap FPC for 1991 was correlated with the top and bottom trap TPM, POC and total pigment fluxes and with the bottom trap PON flux and C:N ratio. The top trap P_{cell} fluxes for 1991 were not correlated with any other trap fluxes, constituents or ratios. The bottom trap P_{cell} fluxes for 1991 were correlated with bottom trap TPM,

Table 3.3. Pearson correlation coefficients matrix showing relationship between different fluxes, constituents and ratios for sediment traps at station C6B during 1991.

	Top TPM	Bottom TPM	Top POC	Bottom POC	Top PON	Bottom PON	Top Pigment	Bottom Pigment	Top Pcell	Bottom Pcell	Top FPC	Bottom FPC	Top TOC	Bottom TOC	Top C:N
Top TPM															
Bottom TPM	0.45														
Top POC	0.64 *	-0.02													
Bottom POC	0.53 *	0.95 *	0.20												
Top PON	0.60 *	-0.04	1.00 *	0.18											
Bottom PON	0.42	0.94 *	0.14	0.98 *	0.13										
Top Pigment	0.79 *	0.12	0.77 *	0.33	0.76 *	0.24									
Bottom Pigment	0.87 *	0.64 *	0.40	0.73 *	0.35	0.61 *	0.69 *								
Top Pcell	0.32	0.26	0.33	0.12	0.32	0.12	0.33	0.17							
Bottom Pcell	-0.06	0.73 *	0.00	0.77 *	-0.06	0.79 *	0.21	0.36	0.14						
Top FPC	0.62 *	0.15	0.79 *	0.35	0.80 *	0.30	0.92 *	0.50 *	0.33	0.32					
Bottom FPC	0.82 *	0.55 *	0.54 *	0.70 *	0.50	0.59 *	0.67 *	0.92 *	0.21	0.38	0.48				
Top % TOC	-0.44	-0.63 *	0.14	-0.54 *	0.17	-0.51 *	-0.19	-0.55 *	-0.12	-0.26	-0.15	-0.35			
Bottom % TOC	-0.46	-0.60 *	-0.24	-0.55 *	-0.21	-0.53 *	-0.19	-0.46	-0.40	-0.45	-0.17	-0.49	0.30		
Top C:N	0.44	0.68 *	-0.04	0.56 *	-0.08	0.54 *	0.03	0.50 *	0.11	0.31	-0.01	0.39	-0.59 *	-0.59 *	
Bottom C:N	0.93 *	0.62 *	0.61 *	0.73 *	0.58 *	0.64 *	0.78 *	0.93 *	0.32	0.42	0.68 *	0.87 *	-0.48	-0.59 *	0.54 *

* significant at alpha error = 0.05
TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
Pcell = phytoplankton carbon flux (Q. Dortch unpubl. data)
FPC = fecal pellet carbon flux (from Chapter 2)
TOC= weight percent of total organic carbon

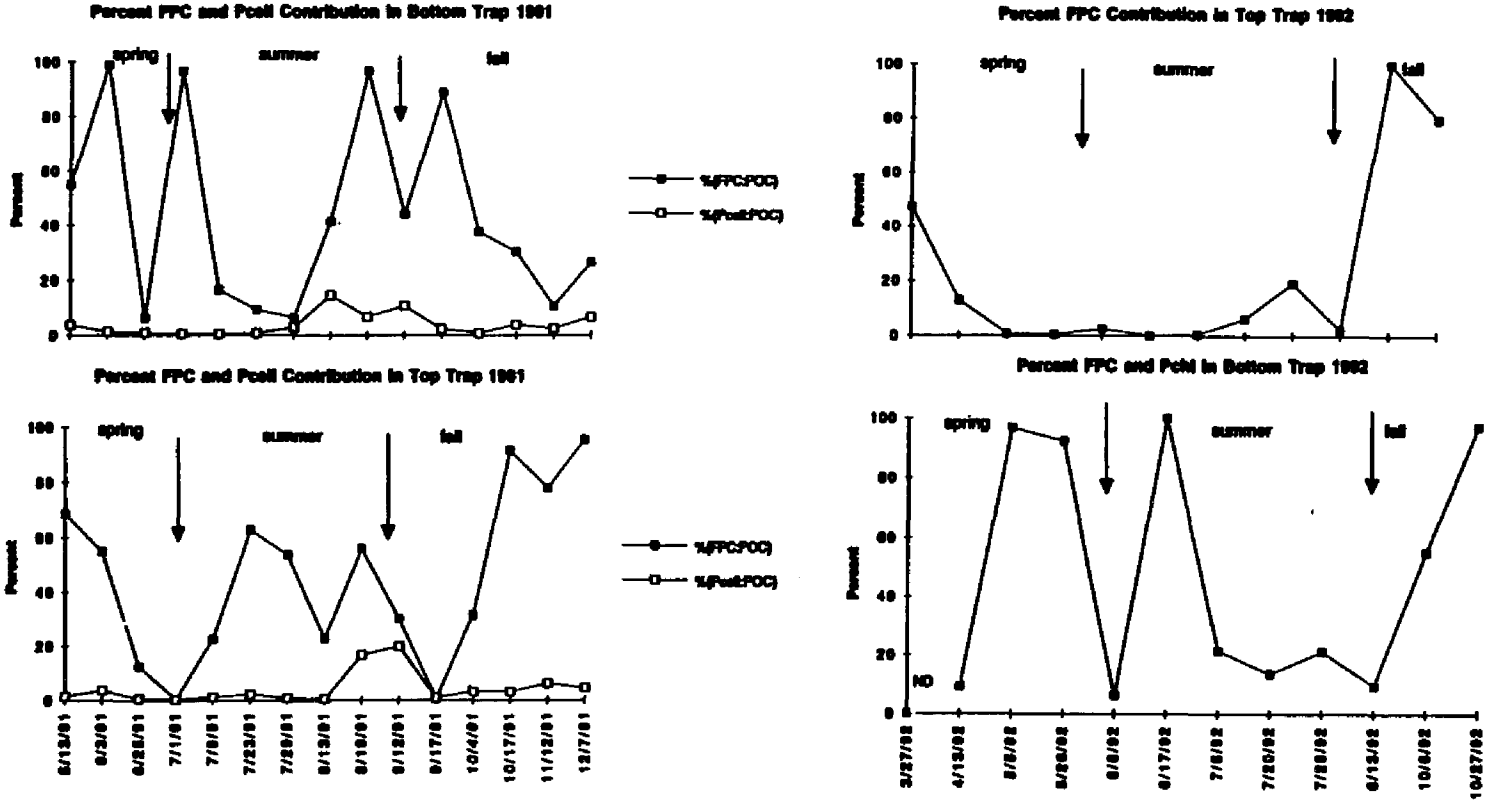


Figure 3.5. Percent contribution of fecal pellet carbon flux to the total particulate organic carbon flux (%FPC:POC), and percent contribution of phytoplankton carbon flux to total particulate organic carbon flux ($\%P_{cell}$: POC) (data presented only for 1991), collected in sediment trap at 5-6 m (top) and 15 m (bottom) depths at station C6B during 1991 and 1992. Arrows delineate dates included in each season; and ND is no data.

POC and PON fluxes. Temporal variations in each of the top trap fluxes (TPM, POC, PON, total pigments and FPC) (Figs. 3.1-3.3) were fairly similar in 1991; consequently, there were positive correlations between most of these variables (Table 3.3). Similarly, the bottom trap fluxes for 1991 (TPM, POC, PON, total pigments and FPC) were all closely related.

There were fewer correlations between sediment trap flux variables in 1992 than in 1991 (Table 3.4). The top trap FPC for 1992 was correlated with top and bottom trap TPM, top trap total pigment fluxes and with the bottom trap POC, FPC and C:N ratio. The bottom trap FPC for 1992 was correlated with the top trap total pigment fluxes and the top and bottom trap TPM and C:N ratio. The top and bottom trap fluxes for 1992 (TPM, POC, PON, total pigments and FPC) were not as closely related to each other as they were in 1991.

A few relationships were consistent across both years. These were: (1) the top trap FPC was related to the top trap TPM and total pigments fluxes and with the bottom trap C:N, and (2) the bottom trap FPC was related to the top and bottom trap TPM and with the bottom trap total pigment fluxes and C:N.

Relationships between Sediment Trap Variables and Environmental Variables

Fluxes of most top trap constituents in 1991 (POC, PON, total pigments, FPC, but not TPM or P_{cell}) were positively correlated with the upper water column dissolved oxygen and total pigment concentrations (Table 3.5). Elevated concentrations of these hydrographic and biological variables would likely be present in spring. Similar relationships were not seen in 1992 (Table 3.6). Fluxes of most bottom trap constituents in 1991 (TPM, POC, PON and P_{cell} (not calculated) but not FPC or total pigments) were positively correlated with the lower water column dissolved oxygen (i.e., mixed water column) and negatively correlated with the lower water column salinity (i.e., stratified water column) (Table 3.5). Similar relationships were seen in

Table 3.4. Pearson correlation coefficients matrix showing relationship between different fluxes, constituents and ratios for sediment traps at station C6B during 1992.

	Top TPM	Bottom TPM	Top POC	Bottom POC	Top PON	Bottom PON	Top Pigment	Bottom Pigment	Top FPC	Bottom FPC	Top TOC	Bottom TOC	Top C:N
Top TPM													
Bottom TPM	0.66 *												
Top POC	0.62 *	-0.11											
Bottom POC	0.26	0.78 *	-0.37										
Top PON	0.54	-0.22	0.99 *	-0.43									
Bottom PON	0.05	0.49	-0.36	0.92 *	-0.39								
Top Pigment	0.83 *	0.79 *	0.30	0.37	0.18	0.12							
Bottom Pigmen	-0.25	0.17	-0.55	0.54	-0.54	0.54	-0.16						
Top FPC	0.73 *	0.96 *	0.00	0.62 *	-0.12	0.34	0.92 *	0.03					
Bottom FPC	0.71 *	0.88 *	0.02	0.56	-0.09	0.28	0.86 *	-0.09	0.92 *				
Top % TOC	-0.37	-0.59 *	0.30	-0.56	0.34	-0.41	-0.22	-0.41	-0.47	-0.43			
Bottom % TOC	-0.51	-0.45	-0.30	-0.18	-0.24	-0.03	-0.49	0.27	-0.49	-0.57	0.08		
Top C:N	0.19	0.88 *	-0.48	0.69 *	-0.54	0.41	0.40	0.39	0.59	0.72 *	-0.68 *	-0.20	
Bottom C:N	0.51	0.77 *	-0.24	0.38	-0.32	0.04	0.61 *	0.01	0.77 *	0.75 *	-0.59	-0.41	0.85 *

* significant at alpha error = 0.05
TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
FPC = fecal pellet carbon flux (from Chapter 2)
TOC= weight percent of total organic carbon

Table 3.5. Pearson correlation coefficients matrix between sediment trap fluxes, constituents and ratios with environmental variables for station C6B during 1991.

	TPM	POC	PON	Pigment	FPC	Pcell	TOC	C:N
Top Trap								
Temp-U	-0.33	-0.06	-0.05	-0.16	-0.29	-0.07	0.63 *	-0.56 *
Salinity-U	0.06	-0.38	-0.42	-0.47 *	-0.36	0.20	-0.48	0.64 *
Dissolved oxygen-U	0.49	0.55 *	0.56 *	0.68 *	0.72 *	0.17	-0.26	0.15
Delta Sigma t	-0.04	0.25	0.28	0.42	0.22	-0.24	0.45	-0.60 *
Chlorophyll a-U	0.21	0.57	0.59	0.61 *	--	0.32	0.02	-0.29
Phaeopigment-U	0.36	0.89 *	0.89 *	0.41	--	0.01	0.47	-0.26
Total pigments-U	0.33	0.85 *	0.87 *	0.63 *	0.82 *	0.22	0.26	-0.33
Salinity-UΨ	-0.25	0.03	0.06	-0.58 *	0.04	-0.11	0.04	0.33
Bottom Trap								
Temp-U	-0.74 *	-0.70 *	-0.79 *	-0.29	-0.14	-0.77 *	0.61 *	-0.46
Temp-L	-0.53	-0.48	-0.60 *	-0.07	0.25	-0.62 *	0.31	-0.19
Salinity-U	0.53	0.35	0.38	0.09	0.17	0.42	-0.47	0.07
Salinity-L	-0.70 *	-0.71 *	-0.77 *	-0.33	-0.45	-0.76 *	0.66 *	-0.44
Dissolved oxygen-U	0.35	0.49	0.54 *	0.36	0.15	0.45	-0.40	0.59 *
Dissolved oxygen-L	0.69 *	0.73 *	0.76 *	0.52	0.42	0.71 *	-0.69 *	0.69 *
Delta Sigma t	-0.59 *	-0.43	-0.49	-0.65 *	-0.25	-0.56	0.54 *	-0.10
Chlorophyll a-U	0.10	0.31	0.37	0.11	--	0.46	-0.23	0.38
Chlorophyll a-L	0.57	0.58	0.70 *	0.02	--	0.82 *	-0.35	0.07
Phaeopigment-U	-0.09	0.08	0.10	0.09	--	-0.06	-0.17	0.33
Phaeopigment-L	0.26	0.39	0.41	0.22	--	0.20	-0.19	0.39
Total pigments-U	0.02	0.25	0.29	0.12	0.41	0.28	-0.24	0.43
Total pigments-L	0.59	0.63 *	0.74 *	0.07	0.20	0.82 *	-0.36	0.14
	0.50	0.41	0.58	-0.33	0.29	0.47	-0.33	-0.09

* significant at alpha error = 0.05
U = averaged for surface and 6.5 m depth
L = averaged for 14 m and bottom
Salinity-UΨ = upper water column salinity lagged one month

TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
Pcell = Phytoplankton carbon flux (Q. Dortch unpubl. data)
FPC = fecal pellet carbon flux (from Chapter 2)
TOC= weight percent of total organic carbon

Table 3.6. Pearson correlation coefficients matrix between sediment trap fluxes, constituents and ratios with environmental variables for station C6B during 1992.

Variables	TPM	POC	PON	Pigment	FPC	TOC	C:N
Top Trap							
Temperature-U	0.22	0.51	0.51	0.01	-0.13	0.19	-0.57
Salinity-U	0.56	0.26	0.19	0.58	0.56	-0.16	0.03
Dissolved oxygen-U	-0.54	-0.43	-0.38	-0.43	-0.36	0.26	-0.09
Delta Sigma t	-0.50	0.01	0.09	-0.81 *	0.86 *	0.24	-0.43
Chlorophyll a-U	-0.51	-0.41	-0.36	-0.45	--	0.08	-0.09
Phaeopigment-U	-0.48	-0.46	-0.42	-0.32	--	0.26	-0.05
Total pigment-U	-0.53	-0.43	-0.38	-0.45	-0.34	0.11	-0.09
Salinity-UW	0.45	0.41	0.35	-0.42	0.31	-0.25	0.11
Bottom Trap							
Temperature-U	-0.23	-0.17	-0.10	0.11	-0.31	0.68 *	-0.51
Temperature-L	0.52	0.47	0.46	0.18	0.47	0.07	0.20
Salinity-U	0.51	0.45	0.48	-0.26	0.69 *	-0.25	0.16
Salinity-L	-0.88 *	-0.89 *	-0.89 *	-0.74 *	-0.66 *	0.04	-0.73 *
Dissolved oxygen-U	-0.34	-0.32	-0.39	-0.35	-0.12	-0.26	0.10
Dissolved oxygen-L	0.72 *	0.68 *	0.59	0.19	0.79 *	-0.57	0.81 *
Delta Sigma t	-0.59	-0.53	-0.55	-0.08	-0.91 *	-0.16	-0.35
Chlorophyll a-U	-0.35	-0.36	-0.42	-0.17	--	-0.23	0.04
Chlorophyll a-L	-0.25	-0.22	-0.19	0.31	--	0.35	-0.41
Phaeopigment-U	-0.20	-0.16	-0.23	-0.01	--	-0.23	0.24
Phaeopigment-L	-0.22	-0.10	-0.07	0.59	--	0.94 *	-0.11
Total pigment-U	-0.34	-0.34	-0.40	-0.15	-0.30	-0.24	0.08
Total pigment-L	-0.31	-0.23	-0.19	0.54	-0.42	0.76 *	-0.36
Salinity-UW	0.20	0.02	0.01	0.03	0.07	-0.10	-0.14

* significant at alpha error = 0.05
U = averaged for surface and 6.5 m depth
L = averaged for 14 m and bottom
Salinity-UW = upper water column salinity lagged one month

TPM = total particulate material flux
POC = particulate organic carbon fluc
PON = particulate organic nitrogen flux
Pigment = total pigment flux
FPC = fecal pellet carbon flux (from Chapter 2)
TOC= weight percent of total organic carbon

1992 for bottom trap TPM, POC, PON, total pigments and FPC, but not P_{cell}, with higher fluxes associated with oxygenated bottom waters and lower fluxes associated with higher bottom water salinities (i.e., stratified).

The best fit models that explain the greatest variability for sediment trap fluxes and %TOC and C:N ratios are given in Table 3.7. Upper water column dissolved oxygen and pigment levels were important in explaining the variability in the top sediment trap characteristics in 1991, but not in 1992. The variability in bottom trap samples in both 1991 and 1992 were explained best by a combination of bottom water dissolved oxygen, temperature and sigma t.

Sediment Resuspension Potential

The measured currents at 1 m above the seabed from May 10 to August 24, 1992 (W. J. Wiseman, Jr. unpubl data) ranged from 3 to 30 cm s^{-1}, and, in only 2-3 short intervals, currents were > 30 cm s^{-1} (Appendix A). The critical velocity required to resuspend 6 ϕ to 1 ϕ sized particles averages 24.5 cm s^{-1} in comparison to fecal pellets which can be resuspended at an average current velocity of 7 cm s^{-1} (Chapter 2: 66). Thus, resuspension of sediments would be less likely during the period of summer currents recorded for 1992. Spring and fall current meter data were not available, but winds from cold front passages that occur more frequently during these seasons, can be potentially high and are sustained long enough to resuspend sediments (Adams et al. 1987).

DISCUSSION

Depth Related Variation

Sediment traps collections are integrated over time and depth. Differences in sedimentation with depth may result from biological and physical processes related to

Table 3.7. Best fit linear regressions for sediment trap fluxes, constituents and ratios with environmental variables at station C6B during 1991 and 1992.

Variables		Model	P > F	r^2	n
Top trap 1991					
LOGTPM	=				
POC	=	- 4020.5 +1703.5 DO-U + 409.9 phaeopigment-U	0.0009*	0.86	15
PON	=	- 638.1 + 109.9 DO-U + 59.29 phaeopigment-U	0.0006*	0.88	15
logFPC	=	5.4 + 2.3 log chlorophyll-U - 1.4 log total pigment-U	0.0405*	0.60	15
Pcell	=	- 3066.9 + 65.8 temperature-U + 235.9 DO-U - 32.8 del sigma t - 15.03 phaeopigment-U	0.0082*	0.91	15
Pigment	=	- 61.52 + 10.2 DO-U	0.0111*	0.58	15
TOC	=	23.3 - 3.2 DO-U + 0.41 total pigment-U	0.0129*	0.71	15
C:N ratios	=	5.38 + 0.076 salinity-U	0.0481-	0.41	15
Bottom trap 1991					
log TPM	=	7.75 + 1.91 log DO-L	0.0011*	0.75	15
POC	=	11260 - 314.5 salinity-L	0.0222*	0.50	15
PON	=	1115.02 - 31.09 salinity- L	0.0111*	0.57	15
logFPC	=	2.9 + 1.64 log DO-L	0.0079*	0.61	15
Pcell	=	607.3 - 5.5 temperature-L - 13.1 salinity-L	0.0008*	0.87	15
log Pigment	=	0.011 + 0.89 log DO-L	0.0226*	0.50	
TOC	=	2.86 - 0.33 DO-L	0.0274*	0.48	15
C:N ratios	=	- 63.7 + 2.01 salinity-L + 1.56 DO-L	0.0266*	0.65	15
Top trap 1992					
log TPM	=	11.05 - 1.15 log total pigment-U	0.0177*	0.53	12
POC					
PON					
logFPC	=	80.2 -18.9 log salinity-U - 6.2 log delta sigma t	0.0018*	0.84	12
Pigment	=	2.63 - 0.27 del sigma t	0.0051*	0.65	12
TOC					
C:N ratios	=	34.81 - 0.78 salinity-U - 0.84 del sigma t	0.0041*	0.79	12
Bottom trap 1992					
LOGTPM	=	1397811 - 39271.6 salinity-L + 7162 DO-L	0.0012*	0.89	11
POC	=	11365 - 314.2 salinity-L + 48.1 DO-L	0.0017*	0.88	11
PON	=	1428.9 - 39.03 salinity-L	0.0015*	0.79	11
logFPC	=	8.84 + 2.11 log delta sigma t	0.0042*	0.64	11
Pigment	=	59.85 - 1.69 salinity-L + 0.24 del sigma t	0.0021*	0.87	11
log TOC	=	0.52 + 0.39 log total pigment-L	0.0120*	0.62	11
C:N ratios	=	45.06 - 1.07 salinity-L	0.0269*	0.53	11

TPM = total particulate material flux
POC = particulate organic carbon flux
PON = particulate organic nitrogen flux
Pigment = total pigment flux
Pcell = Phytoplankton carbon flux (Q. Dortch unpub. data)
FPC = fecal pellet carbon flux (from Chapter 2)
TOC= weight percent of total organic carbon

* significant at alpha = 0.05
U = averaged for surface and 6.5 m
L = averaged for 14 m and bottom

water column stratification, resuspension of sediments, inclusion of zooplankton material in the trap material, and zooplankton behavior. The total particulate material flux in shallow water coastal and open ocean environments is composed partly of material settled from the euphotic zone and partly from resuspended material (Blomqvist & Larsson 1994). Up to 60 to 80% of material collected in bottom traps in coastal environments is fine grained resuspended material (Gardner & Richardson 1994, Blomqvist & Larsson 1994). Because the sediment traps were deployed in a 20-m water column, I determined the potential for sediment resuspension. The potential was extremely low for the mid-summer current meter record available for 1992. The bottom current records for the remainder of the two years of the study were not available, but frequent frontal passages during spring and fall along with sustained winds would likely resuspend and transport sediments then (Adams et al. 1987). Material collected from April to December 1992 from sediment traps deployed within 7 km of station C6B (Gardner & Richardson 1994) was fine grained silt (grain size = 5 ϕ, 60% and 80% of the material collected at 13 m and 19 m, respectively) and was likely material that had been resuspended. These depths are similar to my 15 m trap.

Bottom sediments in the study area are primarily silts with a low total organic content and a high C:N ratio (Chapter 2). Resuspension of sediments would likely produce a dilution effect in the bottom sediment trap with lower %TOC and higher C:N ratios compared to those of the top trap, especially in the spring and fall. The %TOC in bottom trap materials was significantly lower than the %TOC in top trap materials. The %TOC within the bottom trap materials was lower in the fall than the spring and both were lower than in the summer. Similarly, the C:N ratio was significantly higher in the bottom trap materials than the top trap materials, with C:N ratios in the bottom trap being higher in either the fall or the spring compared to the summer. Thus, the quality of material collected in the bottom trap materials was influenced by resuspension of

sediments to a much greater extent than in the top traps, and the potential influence was greater in the fall and/or the spring than in the summer.

Accumulation of bottom sediments in the traps could affect the total particulate material fluxes. Increases in mass flux with depth have been observed in many coastal, shelf and slope environments attributable to turbulent flow near the bottom (Smetacek 1980, Davies & Payne 1984), Harding et al. 1987, Bhosle et al. 1989, Monaco et al. 1990a,b). Overall averages for total particulate material fluxes (TPM) were higher in the bottom trap than in the top trap, and there were seasonal differences that would indicate the effects were primarily seen in the bottom traps. The TPM in fall 1991 was much greater in the bottom trap than in the top trap. Both the spring and summer TPM fluxes in the top traps exceeded those of the bottom traps, but these were primarily biological materials (i.e., mass attributable to POC and PON fluxes were higher in the top traps than the mass in the bottom traps contributed by sediments). The bottom trap TPM exceeded that of the top trap in 1992, especially in the spring and fall. The seasonal differences observed in the top trap in 1991, related to higher phytoplankton biomass in the surface waters, were not seen during 1992.

Other differences were found in sediment trap collections from the upper water column versus the lower water column that were not necessarily related to the potential of sediment resuspension. The average fluxes of POC, PON, FPC, P_{cell} and total pigments (and TPM for spring and summer of 1991) were greater in the top traps than in the bottom traps. The %TOC was higher in the top traps than the bottom traps, and the C:N ratio was higher in the bottom traps than in the top traps (as mentioned above). Lower fluxes of POC and PON in the bottom trap could be due to bacterial remineralization of sinking particulate material in the water column. The top trap C:N ratios were especially lower than in the bottom trap in the summer (Fig. 3.4). Higher C:N ratios in the bottom trap materials might represent the preferential removal of nitrogen in comparison to carbon by bacterial remineralization and recycling within the

bottom water. Alternatively, or in addition, the decrease in %TOC with depth and negative correlations between %TOC and TPM, POC, PON and total pigment fluxes for the top and the bottom trap indicate that particulate carbon is not the only mechanism for carbon export from the surface layer. Some unknown fraction of dissolved organic carbon may leach out of particulate material by diffusive and advective processes (Knauer & Asper 1989, Lee et al. 1992, Peterson et al. 1993, Miquel et al. 1994).

The higher POC, PON, FPC and P_{cell} fluxes into the top traps compared to the bottom traps indicates that more biogenic particles (including zooplankton) flux through the upper water column than the lower water column. The depth related differences in FPC and P_{cell} fluxes were not statistically significant, but those for POC and PON were. A preservative (glutaraldehyde) used to inhibit degradation of organic material within the trap may have attracted zooplankton 'swimmers' (Lee et al. 1988, Lee et al. 1992) that are known to cause problems in sediment trap sampling (Knauer et al. 1979, 1984, Karl & Knauer 1984, Skjoldal & Wassmann 1986, Lee et al. 1988) and create ambiguity as to what is the true flux. The longer deployments for our study necessitated the use of a preservative to prevent organic degradation so that the actual flux could be measured (Gardner et al. 1983, Wakeham et al. 1993, Hedges et al. 1993). Any trap preservative treatment that effectively limits microbial activity usually results in some swimmer artifact (Wakeham et al. 1993). Detrital and whole zooplankton material were present in the sediment trap samples; their presence was more frequent during the summer and in the top trap.

Microscopic hand picking and removal of the 'swimmers' has been used and recommended, but may not always be satisfactory (Knauer et al. 1984, Knauer & Asper 1989, Michaels et al. 1990, Lee et al. 1992). It is difficult to distinguish between 'swimmers' and 'sinkers', and removal of zooplankton by any physical barrier tends to underestimate a significant portion of flux that is contributed by 'sinkers'. Possible

mechanisms for including zooplankton in traps include: sinking of dead organisms into the trap, flocculation of material or formation of 'marine snow' that includes zooplankton carcasses, exuviae, fecal pellets and other detrital material, as well as some active 'swimmers' being trapped in the snow or being directly trapped in the sediment trap (Knauer & Asper 1989). The exact designation of 'swimmer' against 'sinker' is very difficult and therefore, in this study, only organisms larger than 5 mm were picked during sample handling, and smaller zooplankton particles in the sample were retained. An exception to this procedure was that during the massive sedimentation of pteropods in the June 6 through July 6, 1992 samples it was not possible to remove all the organisms without also removing attached particulate materials. Comparatively more zooplankton in the top trap in the spring and the summer may be related to the greater abundance of zooplankton abundance in the water then (Chapters 4 and 5) and potentially greater POC and PON fluxes in the top trap.

Seasonal Variability

The flux of materials (TPM, POC, PON, FPC, P_{cell} and total pigments) varied between seasons, with higher sedimentation in either spring or fall compared to summer (Fig. 3.1, Table 3.2). [Higher fluxes of TPM into the bottom traps, especially in the fall periods, is most likely the result of sediment resuspension (see above).] There were also inter-annual differences, with fluxes of all the above being greater in 1991 than in 1992 (except P_{cell} which was not calculated for 1991). Spring is characterized by high primary and net production (Lohrenz et al. 1990, Justic' et al. 1993). The spring freshet of the Mississippi River was much higher in 1991 (20,000-35,000 m^3 s^{-1}) than in 1992 (10,000-20,000 m^3 s^{-1}) at Tarbert Landing, Mississippi (Dinnel 1993). High fluxes occurred in spring 1991 compared to fall, and both spring and fall 1991 fluxes were higher than those in summer. Spring fluxes in 1992, while higher than fall and summer, were not as high as in spring 1991. The POC and PON fluxes in the upper water

column might be high in spring (sometimes in summer) in 1991 because of the horizontal advection of organic material produced in the Mississippi River plume region that moved downfield in a westward direction (Rabalais et al. 1994b). However, significant and positive correlations between top and bottom trap fluxes indicate that material collected in the top trap and the bottom appeared to be derived from the same surface production. High spring Mississippi River discharge occurred in late May 1991 (Chapter 1, Fig. 1.2), likely stimulating higher primary production that lagged temporally and spatially by one month resulting in higher fluxes. The total Mississippi River discharge in 1992 was considerably less than in 1991 (Dinnel 1993). If the general relationship of one month lagged surface water net productivity to the peak river flow (Justic' et al. 1993) existed for 1991, then the higher fluxes of organic material indicate a riverine influence on the amount of material collected in the sediment traps.

The linkage of particulate material flux and surface production cycles has been reported for other areas (Eppley & Peterson 1979, Deuser & Ross 1980). Given that productivity in the euphotic zone will regulate the vertical flux of biogenic as well as abiogenic particles in the ocean (Deuser et al. 1981, 1983, Honjo 1982), it is logical to expect higher sedimentation from the euphotic zone in an area of a higher integrated primary productivity (IPP) (Eppley & Peterson 1979, Walsh et al. 1989).

Another factor that can contribute to the temporal difference in the sedimentation of particulate materials from the surface is a difference in the phytoplankton community (Redalje et al. 1994). The sediment trap sampling started in mid-April 1991 and early March 1992. It is possible that a massive sedimentation of a spring bloom was not captured, especially in 1991. A seasonal change in species composition from large heavily silicified diatoms to lightly silicified diatoms (because of possible silica limitation) has been observed especially in surface waters in a gradient away from the river plume (Dortch et al. 1992, unpubl. data). Dortch et al. (1992)

measured phytoplankton flux into floating traps deployed in the Mississippi plume region and hypoxic shelf region, and into moored traps at station C6B in spring and fall 1990. The phytoplankton flux was an order of magnitude higher in the plume region than in the hypoxic region and was comprised mostly of diatoms (*Skeletonema costatum*). The temporal changes in species composition from a higher flux of diatoms in spring (likely to be silicate limited in late spring Q. Dortch pers. comm.) to lower fluxes in summer and fall were observed in the moored traps (Dortch et al. 1992) and may follow seasonal progression of diatom population abundances (Dortch 1994).

On the other hand, both fecal pellet carbon and phytoplankton carbon fluxes were lower in summer than in spring and fall. This is likely related to the reduction in food availability (phytoplankton biomass in the surface waters) and/or retention and remineralization of particles in the upper water column of a highly stratified system. The %FPC of the total particulate carbon was also less in summer than spring and fall. Although there were no statistically significant seasonal differences in the $\%P_{cell}$ contribution to POC fluxes, there were somewhat higher P_{cell}:POC ratios in late summer and early fall in both the top and the bottom traps. These may result from the sedimentation of larger aggregates formed during this period (obvious, large marine snow aggregates observed by SCUBA divers, N. N. Rabalais, pers. comm.) that facilitate the flux of smaller phytoplankton cells that predominate (e.g., cyanobacteria, Q. Dortch pers. comm.).

Differences in mesozooplankton grazing and microzooplankton grazing can affect the amount of POC exported to the seabed (Redalje et al. 1994). Dagg and Ortner (1992) found higher mesozooplankton community ingestion rates in July/August 1990 in the plume region than in the shelf/hypoxic region and concluded that one of the principal fates of the primary production was to be grazed by the mesozooplankton community. Microzooplankton grazing rates were higher in summer (July/August 1990) than in spring (March 1991) (Dagg & Ortner 1992, Fahnenstiel et al. 1992).

High microzooplankton grazing was linked to higher ammonium regeneration rates in July/Aug 1990 than in March 1991 (Benner et al. 1992, Gardner et al. 1994). Low export of primary production as POC in summer, when microzooplankton grazing rates and bacterial regeneration rates were higher, suggests a tightly coupled heterotrophic system where production was closely coupled with regenerated production, which would result in low POC export from the surface. Grazing by microzooplankton produces small fecal pellets with negligible sinking rates (Stoecker 1984) and results in lower losses via sedimentation. In comparison, a high %IPP exported from the surface layer in spring could be related to low microzooplankton grazing and low bacterial regeneration rates (Redalje et al. 1994). Mesozooplankton grazing is more likely to dominant during spring especially in the coastal region (Ortner et al. 1989) when primary production is grazed and integrated into fecal pellets that have faster sinking rates and could increase the organic load to the sea floor.

Relationships between Fluxes

There were highly significant and positive correlations between TPM, POC, PON, total pigment and FPC fluxes in both the top and the bottom trap which indicated that sedimentation rates of the components were related with each other (Tables 3.3 and 3.4). This result demonstrates the importance of surface waters as a source of material found in both the top and the bottom traps. The significant negative correlation between %TOC and TPM, POC, PON, total pigment, FPC fluxes in the top and the bottom traps in 1991 indicates that the particulate material caught in the trap was derived from material lower in %TOC, due to loss of soluble organic and inorganic components within the water column and/or dilution of trap material (especially near the bottom) from resuspended material of low organic content (Peterson et al. 1993). The negative, but not always significant, correlation in 1992 (Table 3.3 and 3.4) also indicates a biogenic origin. The average %TOC in the top trap was 10% and reached

up to 30% during summer, indicating that the possible source of particles reaching the traps was biogenic (zooplankton) material produced in the water column (Buscail et al. 1990, Peterson et al. 1993).

The significant and positive correlation between fecal pellet carbon flux and the total pigment flux in both traps in 1991 and in the top trap in 1992 (Tables 3.3 and 3.4) may be the result of herbivore grazing and defecation (Lorenzen et al. 1983, Welschmeyer et al. 1984). The positive correlation between total pigment and FPC fluxes indicates a higher grazing rate associated with higher primary productivity. High mesozooplankton grazing rates have been measured from this region (Dagg & Ortner 1992). Zooplankton grazing control on phytoplankton has been suggested for some time (Harvey et al. 1935). If zooplankton grazing is not coupled with the phytoplankton production, especially during bloom development, a massive sedimentation of phytoplankton cells may result. There were significant and positive correlations between P_{cell} flux in the bottom trap and TPM, POC, and PON fluxes in the bottom trap (Table 3.3). The P_{cell} flux, although positive, was not significantly correlated with fecal pellet carbon flux in 1991 ($r^2 = 0.21$ to 0.38, Table 3.5) and indicates higher grazing and production of fecal pellets when primary production was high. The positive relationship between fluxes in the bottom trap indicate fluxed particulate material was likely originating from the surface primary production.

Relative Importance of Fecal Pellet Carbon (FPC) and Phytoplankton Carbon (P_{cell}) Fluxes to the Export of Primary Production

Redalje et al. (1994) used floating sediment traps for short (1 to 2 d) deployments and observed high variability in the ratios of POC flux to integrated primary production (IPP) in the Mississippi River plume and adjacent shelf (hypoxic) regions. They observed high ratios of export of particulate organic carbon when IPP was low and low ratios when IPP was high (Redalje et al. 1992, 1994). Considerable

variability exists in primary production within the study area (Lohrenz et al. 1990), and, therefore, greater temporal information is needed to find a conclusive relationship between rates of IPP and POC export ratios.

Redalje et al. (1994) found low ratios of POC export to IPP when the system was highly stratified compared to high ratios when the system was mixed. High POC export when IPP was low, and vice versa, indicated that other factors may affect the export ratio. Horizontal advection of particulate material is one likely factor. Rabalais et al. (1994b) found a significant correlation between two days lagged daily averaged dissolved oxygen data at C6A (near my study site C6B off Terrebonne Bay) and daily averaged data from station WD32E, situated 77 km east and closer to the Mississippi River delta. They suggested that downplume transport brought organic material derived from areas where phytoplankton biomass is three to seven times greater (Dagg & Whitledge 1991, Hitchcock & Whitledge 1992, Rabalais et al. unpubl. data) than at the shelf station (C6A or C6B). [N.B., the sinking rate of mesozooplankton fecal pellets is on the order of 10^1 to 10^3 m d^{-1} (Bienfang 1980, Madin 1982, Laws et al. 1988, Dilling & Aldredge 1993).]

Although no simultaneous primary production data were taken to provide a direct comparison at the study site between fluxes and primary production, IPP data from previous studies were used to determine the range of relationships between surface primary production and fluxed carbon. Monthly primary production data from the southeastern shelf region (Sklar 1976) were used to obtain integrated primary production for the seasonal periods corresponding to the 1991-1992 sediment trap data. The data of Sklar (1976) were collected in the early 1970s, which is a mid-point in the period from the early 1950s to the early 1990s, during which nutrient concentrations and ratios in the lower Mississippi River changed dramatically (Turner & Rabalais 1991) and overall productivity in the surface waters increased as a consequence (Turner & Rabalais 1994). As a consequence of these nutrient changes and biological

responses, the IPP values used (i.e., Sklar 1976) may be an underestimation of the current primary production rates.

I estimated the fraction of integrated primary production that would be exported out of the surface layer in each season (spring, summer and fall) by comparing the 1991-1992 FPC and P_{cell} fluxes to seasonal averages of IPP (Sklar 1976). The ratios of POC, FPC and P_{cell} to estimates of surface primary production are given in Table 3.8. The ratio of POC flux to primary production ranged from 10 to 277%; the average for both years was 40% at 6 m and 25% at 15 m depth. The ratio of the flux of fecal pellet carbon to estimated primary production ranged from 1 to 128%; the average for both years was 19% at 6 m and 15% at 15 m depth. Similar calculations showed that the ratio of the flux of phytoplankton carbon (P_{cell}) to primary production ranged from 0.24 to 8.6% ; the average for both years was 4.4% at 6 m and 1.9% at 15 m depth. The fraction of primary production exported in POC varied with season and was higher than other shallow water regions but comparable to other data from the area (Table 3.9) which ranged from 6% in July/August 1990 to 270% in March 1991 (Redalje et al. 1992, 1994).

The amount of organic material exported varied considerably during the two years (Table 3.8). For example, the flux of POC in spring 1991 exceeded twice the estimated IPP, and the FPC flux accounted for a large fraction (127%) of the estimated IPP into the top trap compared to the bottom trap. The POC flux into the bottom trap was nearly half (47%) of the estimated IPP of which FPC flux comprised 29%. The ratio of POC fluxed to the estimated primary production was lower in summer than in spring and fall; ratios were 28% for the top trap in summer and a third of that amount (10%) for the bottom trap. The fraction of estimated primary production exported in POC flux in fall 1991 was very high (277%) in the top trap and exceeded almost three times the IPP; the amount of POC exported for the bottom trap was two times the estimated IPP (191%). The pattern was different in 1992. The percent export of

Table 3.8. Average particulate organic carbon (POC), fecal pellet carbon (FPC) and phytoplankton carbon (Pcell) fluxes measured in top (5-6 m) and bottom (15 m) sediment traps at station C6B, and estimated percent fraction of integrated primary productivity (IPP) during 1991 and 1992; nd= no data.

	POC gC/m^2/d	POC gC/m^2/d	FPC gC/m^2/d	FPC gC/m^2/d	Pcell gC/m^2/d	Pcell gC/m^2/d	Days in season	IPP/season* g C/m^2/season
	5 - 6 m	15 m	5 - 6 m	15 m	5 - 6 m	15 m		
1991								
spring	3.73	0.79	2.17	0.50	0.07	0.02	60	101.62
summer	0.49	0.18	0.16	0.07	0.01	0.004	60	105.09
fall	1.42	0.98	0.41	0.34	0.07	0.04	90	46.00
1992								
spring	0.50	0.27	0.03	0.18	nd	nd	75	120.42
summer	1.32	0.46	0.02	0.09	nd	nd	75	120.00
fall	1.06	0.87	0.93	0.62	nd	nd	45	37.00

	POC/IPP %	POC/IPP %	FPC/IPP %	FPC/IPP %	Pcell/IPP %	Pcell/IPP %
	5 - 6 m	15 m	5 - 6 m	15 m	5 - 6 m	15 m
1991						
spring	219.94	46.82	127.95	29.29	4.09	1.02
summer	28.03	10.11	9.36	4.05	0.55	0.24
fall	277.24	190.96	79.43	65.74	8.64	4.67
1992						
spring	31.06	16.82	1.81	11.09	nd	nd
summer	82.55	28.50	1.31	5.56	nd	nd
fall	128.60	106.30	113.35	75.41	nd	nd

* estimates of IPP for each season are summed monthly data to match sediment trap seasons (Sklar 1976)

Table 3.9. Comparison of sediment trap fluxes (g/m^2/d) for total particulate material (TPM), particulate organic carbon (POC) and the fraction of primary production (PP) exported (POC:IPP) in shallow water regions.

Location	Depth of trap (m)	PP (g C/m^2/d)	TPM (g/m^2/d)	POC (g C/m^2/d)	POC:IPP (%)	Source
Departure Bay B. C., Canada	30	0.55	8.22	0.55	100	Stephens et al. 1967
Loch Ewe, Scotland	30	0.25		0.16	64	Steel & Baird 1972
Bedford Basin, N. S., Canada	20	0.603	2.16	0.16	27	Hargrave et al. 1976
	70	0.55		0.21	38	Hargrave & Taguchi 1978
Lindaspollene (Fjord) Norway	10	0.26	1.16	0.14	54	Wassmann 1983
Dabob Bay, Puget Sound	110	0.53		0.29	55	Welschmeyer & Lorenzen 1985
a. Plume region	15	4 to 8		0.3 to 1.8	3 to 225	Redalje et al. 1994
b. Hypoxic region Gulf of Mexico	15	0.12 to 3		0.18 to 0.4	6 to 270	
Inner continental Shelf,	*5 to 6*		*1.5 to 138*	*0.12 to 7*	*31 to 277**	*This study*
Gulf of Mexico	*15*		*3.3 to 289*	*0.06 to 1.9*	*10 to 191**	

* monthly primary production data from Sklar (1976)

estimated IPP via POC was much lower in spring (31%) in the top trap and was nearly half in the bottom trap (17%). The high %POC:IPP seen in fall 1991 was paralleled by high ratios in both top and bottom traps in 1992, 129% and 106%, respectively.

One pattern that emerged from this study and Redalje et al.'s (1994) is that the export ratios were lower in summer when the water column was more strongly stratified. Low fluxes associated with stratified water columns have been reported for shallow coastal waters in the northern Adriatic Sea (Puskaric et al. 1992). Physical features such as density stratification, either with a thermocline or halocline, were associated with the retention and recycling of particles within the upper water column. The importance and effect of water column density structure on particulate fluxes has also been observed for the open ocean in the Ligurian sea off Corsica, where three to four times higher fluxes were observed during periods when the water column was mixed than during the stratified period (Miquel et al. 1994).

The highest %FPC:IPP ratios were in the top trap in 1991, especially in spring (127% of total estimated IPP). The highest $\%P_{cell}$:IPP was in the top trap and peaked in fall in the top trap (Table 3.8). The %FPC:IPP in 1992 was very low (2%) and was lower in the top trap than in the bottom trap; the highest ratio occurred in fall in the top trap (Table 3.8). The low %FPC:IPP corresponded to a low POC:IPP ratio in 1992; however, the higher POC:IPP ratios in the spring and summer (especially in the summer) corresponded to the capture of pteropod shells in the upper water column trap which influenced the POC flux. The high ratio of FPC fluxes to estimated primary production emphasizes that the importance of seasonally variable grazing by meso- and microzooplankton as the system alters between an exporting and a recycling system.

The comparison of export ratios with available seasonal data (Sklar 1976) showed variation in fluxes with seasons were closely related to biological and physical processes. The biological and physical processes on the Louisiana continental shelf are under the influence of Mississippi river flow. Biological factors influence the export

ratios through various mechanisms, phytoplankton and zooplankton community structure, that will affect phytoplankton cell flux, fecal pellet carbon flux, and therefore, particulate organic carbon flux. The importance of export of primary production from the surface waters alternates with the importance of recycling remineralization processes. These processes are regulated by physical processes, and hydrodynamic singularities that occur over a wide range of spatial and temporal scales and play a major role in favoring export of primary production to *in situ* recycling processes (Miquel et al. 1994). Examples of hydrodynamic singularities on the vertical scale include pycnoclines, and eddies, fronts and upwelling regions on the horizontal scale, and temporal transitions in vertical stability structure with periodicities ranging from annual to semidiurnal (tidal) and sometimes smaller (Langmuir circulation) (Legendre & Le Ferve 1989). Legendre and Le Ferve (1989) explained that new and regenerated production, given their different temporal and spatial scales, could operate side by side in a bifurcation model. The fate of primary production appears to follow the five bifurcation model where production is channeled into export pathways and hydrodynamic singularities play an important part at each bifurcation to favor export or recycling of primary production (Legendre & Le Ferve 1989). In their model, the first bifurcation sets a condition for production of large phytoplankton that are expected to rapidly sink from the euphotic region. The second bifurcation sets a condition for entrainment of larger phytoplankton cells at density gradients (pycnoclines), or channeled into different heterotrophic pathways. The third bifurcation sets a condition where larger cells do not sink but are transferred to higher trophic levels, or are remineralized in the upper water column due to coupling or uncoupling resulting in changes in pelagic food chains. The fourth bifurcation gives a condition under which very small cells are produced and instead of entering the microbial loop are aggregated and channeled to higher trophic levels. At the fifth bifurcation, the aggregates either sink and provide a source of organic matter to the lower water column or seabed or are

recycled in the euphotic zone. These conditions are set by different hydrodynamic processes occurring at various spatial and temporal scales that control the relative importance of export versus recycled production in oceans (Legendre & Le Ferve 1989).

Potential of Fecal Pellet Carbon (FPC) and Phytoplankton Carbon (P_{cell}) Fluxes to Induce Hypoxia

Justic' et al. (1993) estimated an oxygen depletion rate of 2.4 ml O_2 l^{-1} $month^{-1}$, by assuming a sedimentation to primary production ratio of 0.5 for the shelf area (Rabalais et al. 1991) and an RQ of 1, and estimated that 412 g O_2 m^{-1} yr^{-1} can be consumed by benthic and epibenthic respiration. Oxygen depletion rates were estimated using the same assumptions from POC and FPC fluxes collected in the sediment traps (Table 3.10). The potential oxygen depletion rates in spring were higher (0.30 and 0.10 ml O_2 l^{-1} d^{-1}, at 15 m depth in 1991 and 1992, respectively) than the apparent oxygen depletion rate (0.08 ml O_2 l^{-1} d^{-1}) calculated by Justic' et al. (1993). The potential oxygen depletion rate for fecal pellets collected in the bottom trap (0.18 ml O_2 l^{-2} d^{-1}) was high in spring 1991, and the amount of fecal pellet carbon flux in spring in the bottom trap appeared to be sufficient to induce hypoxia. The potential oxygen depletion rate for P_{cell} flux at 15 m depth was low, 0.006 ml O_2 l^{-2} d^{-1}, and was much lower in the summer. These lower rates were not sufficient to induce hypoxia but may add to fecal pellet carbon and deplete oxygen in the bottom waters. The potential oxygen depletion rate in summer was low because FPC flux (and POC flux) was low in summer. It appears that respiration of POC and FPC fluxes in spring will create low dissolved oxygen bottom waters or hypoxia, and this hypoxia is then sustained and maintained through summer in a stratified water column. Although the flux of FPC (and POC flux also) and the oxygen depletion rates were also high in fall, the vertical

Table 3.10. Relationship of particulate organic carbon (POC), fecal pellet carbon (FPC), and phytoplankton carbon (Pcell) fluxes with oxygen depletion rates based on carbon fluxed at 5-6 m and 15 m depths at station C6B during 1991 and 1992. Analysis assumes: (1) all C is respired, not buried or in biomass or organisms, and (2) only vertical fluxes deliver carbon to the lower water column and seabed.

	POC 5 - 6 m	POC 15 m	FPC 5 - 6 m	FPC 15 m	Pcell 5 - 6 m	Pcell 15 m
Fluxes:	mgC/m^2/d	mgC/m^2/d	mgC/m^2/d	mgC/m^2/d	mgC/m^2/d	mgC/m^2/d
1991						
spring	3725	793	2167	496	69	17
summer	491	177	164	71	10	4
fall	1417	976	406	336	66	36
Average	1878	649	912	301	48	19
1992						
spring	499	270	29	178	nd	nd
summer	1321	456	21	89	nd	nd
fall	1057	874	932	620	nd	nd
Average	959	533	327	296	nd	nd
Potential Oxygen Depletion Rates*						
1991	ml O2/l/d	ml O2/l/d	ml O2/l/d	ml O2/l/d	ml O2/l/d	ml O2/l/d
spring	0.46	0.30	0.27	0.18	0.009	0.006
summer	0.06	0.07	0.02	0.03	0.001	0.002
fall	0.18	0.36	0.05	0.13	0.008	0.013
Average	0.23	0.24	0.11	0.11	0.01	0.01
1992						
spring	0.06	0.10	0.01	0.07	nd	nd
summer	0.16	0.17	0.01	0.03	nd	nd
fall	0.13	0.33	0.12	0.23	nd	nd
Average	0.12	0.20	0.04	0.11	nd	nd

* oxygen depletion rate of 0.08 ml O2/l/d, based on 50% sedimentation (Justic' et al. 1993).

mixing of the water column because of cold front passages breaks down the density stratification and keeps the water column well mixed and oxygenated (Table 3.10).

The fecal pellet carbon flux into the bottom trap was low in spring in 1992. The oxygen depletion rate for this FPC flux was 0.07 ml O_2 l^{-2} d^{-1}, close to the calculated oxygen depletion rate (0.08 ml O_2 l^{-2} d^{-1}) (Table 3.10). Phytoplankton carbon flux data are not available for 1992 to calculate the resulting oxygen depletion rates. However, the POC flux into the bottom trap in spring 1992 (which includes phytoplankton) is high enough to induce hypoxia that is sustained through the stratified summer period. The 1992 P_{cell} flux data may show a greater contribution of fluxed carbon via sinking phytoplankton cells that may have been missed in 1991, because sampling started later in the year (April 17, 1991 cf. March 2, 1992). A massive flux of ungrazed phytoplankton cells in the spring cannot be ruled out as a source of carbon fueling hypoxia, but flux calculations for the spring through fall period of 1991 indicated that fecal pellet carbon flux far exceeded the contribution of carbon to the seabed by phytoplankton cells. The results support the hypothesis that development of summer hypoxia is associated with the decomposition of organic matter accumulated in spring primarily by the sedimentation of a phytoplankton bloom via fecal pellets rather than as intact phytoplankton cells.

CONCLUSIONS

Moored sediment traps were deployed in a 20-m water column on the continental shelf influenced by the effluent of the Mississippi River and subject to seasonally severe hypoxia. Fluxes of total particulate material (TPM), particulate organic carbon and nitrogen, total pigments, fecal pellet carbon (FPC) and phytoplankton carbon (P_{cell}) (one year only) were measured over a 2-yr period within the upper (~ 5-6 m = top) and lower (16 m = bottom) water column.

The average fluxes of total particulate material, particulate organic carbon and fecal pellet carbon (Chapter 2) were high compared to other coastal regions. Estimates of the proportion of primary production exported in POC were also higher than other shallow water regions, but comparable to previous estimates (short-term deployments) from the area (i.e., less spatial and temporal information). Highly significant and positive correlations between TPM, POC, PON, total pigment and FPC fluxes in both the top and the bottom traps indicated that sedimentation rates of the components were related to each other. This result also suggested the importance of surface waters as a source of material sedimented into both traps.

The flux of TPM, POC, PON, FPC, P_{cell} and total pigments varied similarly between seasons, with lowest sedimentation in summer. There were also inter-annual differences, with fluxes of all the above (except P_{cell} which was not calculated for 1991) being greater in 1991 than in 1992. Higher fluxes of TPM into the bottom traps, especially in the fall, was most likely the result of sediment resuspension, as identified from dilution of the trap materials with sedimentary %TOC and C:N ratios. Surface fluxes were positively correlated with indicators of high surface water production (dissolved oxygen and pigment concentrations) for the 1991 series, but not for 1992. High surface water production occurs in spring, and the yearly differences in the strength of relationships to indicators of surface water productivity can be related to the differences in the spring freshet of the Mississippi River, which was much greater in 1991 than in 1992. Fluxes of most bottom trap materials were positively correlated with the lower water column dissolved oxygen (i.e., mixed water column) and negatively correlated with the lower water column salinity (i.e., stratified water column). Fecal pellet carbon flux contributed approximately 55% of the particulate organic carbon flux. The flux of fecal pellet carbon in the spring is likely directly related to food availability. Lower fluxes in summer, during periods of greatest stratification, may be due to the retention or remineralization of fecal pellets in the

upper water column. Higher overall fluxes of most constituents in the fall compared to summer may result from resuspended sediments. The evidence for resuspension was greater in the fall, especially in the bottom traps.

Fecal pellet carbon flux was higher in both traps than the phytoplankton carbon flux (1991 comparison), except for a single sample. The differences were not statistically significant for the top trap but were for the bottom trap. The same seasonal trends were seen in phytoplankton carbon flux and in fecal pellet carbon flux. The contribution of fecal pellet carbon to the particulate organic flux ranged from near 0 to 100%, but averaged 55%. The phytoplankton carbon flux contribution to particulate organic carbon flux was substantially lower and ranged from near 0 to 17%, and averaged 4%. The relative differences between FPC and P_{cell} fluxes were most pronounced in spring, somewhat lower in summer, and lowest in fall. Comparative data for these fluxes were available only for 1991, when sediment trap deployments began in mid-April. A massive flux of ungrazed phytoplankton cells from high surface production earlier in the spring cannot be ruled out, but peak river flow occurred later in spring 1991 than normally (early May cf. March to April, Fig. 1.2). The long-term trend is for net surface water production to lag one month behind peak river flow and for bottom water oxygen deficiency to lag two months behind peak river flow (Justic' et al. 1993). Overall, the flux of fecal pellet carbon to the seabed far exceeded that of phytoplankton cells. A massive sedimentation of carbon via phytoplankton cells is unlikely to occur, because the surface primary production is not uncoupled from grazing as in northern latitudes. Several features of the system indicate that it is closely coupled: (1) abundant zooplankton grazers exist, even in spring (Chapters 4 and 5), (2) mesozooplankton grazing rates are high, (3) the larger fecal pellets that are more likely to sink are produced, and (4) even if grazing does not substantially reduce the phytoplankton standing stock, sufficient fecal pellet production occurs to facilitate a high percentage of the surface water primary production to the seabed. The ratios of

fecal pellet carbon flux to estimated primary production averaged 19% at 5-6 m and 15% at 15 m depth; those for phytoplankton carbon flux were 4% and 2%, respectively. Export ratios were lowest in summer when the water column was stratified.

I estimated oxygen depletion rates for the carbon fluxed at 5-6 m and 15 m for particulate organic carbon, fecal pellet carbon and phytoplankton carbon. The oxygen depletion rate for fecal pellets collected in the bottom trap was high in spring 1991 and far exceeded the potential rate due to phytoplankton carbon. Fecal pellet carbon fluxes in spring 1991 were sufficient to create low dissolved oxygen bottom waters or hypoxia which is then sustained and maintained through the summer in a stratified water column. The fecal pellet carbon flux into the bottom trap was low in spring in 1991 and phytoplankton carbon flux was not calculated. However, POC flux (which includes both fecal pellet and phytoplankton carbon) was sufficient to deplete the bottom water oxygen. A massive sedimentation of phytoplankton cells cannot be ruled out for 1992, but fecal pellet carbon far exceeded the contribution of carbon to the seabed by phytoplankton cells in 1991. POC and PFC fluxes were lower in summer, but also sufficient to deplete oxygen, especially if the concentrations were already lower. The data and calculations support the hypothesis that development of summer hypoxia is associated with the decomposition of organic matter accumulated in spring primarily by the sedimentation of a surface water organic material via fecal pellets, rather than as intact phytoplankton cells.

The export of carbon from surface waters to the lower water column and sediments on the southeastern Louisiana shelf in the influence of the Mississippi River is high (approximately 67%) and exceeds the estimate of Suess (1980) for coastal waters. Of the particulate material exported vertically, 55% is contained in fecal pellets. The carbon fluxed via fecal pellets is sufficient to deplete the bottom water oxygen reserves in spring, thus creating hypoxic conditions that then prevail through the stratified summer period. Lower fluxes of organic material in summer are sufficient

to deplete dissolved oxygen concentrations, especially if they are already delpeted. Temporal and spatial variability is high on the continental shelf adjacent to the Mississippi River. Long term deployments, like this data set that encompassed over two years (approximately 66 to 70% of each year), were amenable to statistical analyses that facilitated identification of seasonal trends of the important biological processes and carbon budgets for a riverine influenced continental shelf.

REFERENCES

ADAMS, C. E., JR., D. J. P. SWIFT, AND J. M. COLEMAN. 1987. Bottom currents and fluviomarine sedimentation on the Mississippi prodelta shelf: February-May 1984. J. Geophy. Res. **92**: 14595-14609.

ALLDREDGE, A. L., AND C. C. GOTSCHALK. 1989. Direct observations of mass flocculation of diatom blooms: characteristics, settling velocities and formation of diatom aggregates. Deep-Sea Res. **32**: 159-171.

BENNER, R., G. CHIN-LEO, W. GARDNER, B. EADIE, AND J. COTNER. 1992. Fate and effects of riverine (and shelf-derived) dissolved organic matter on Mississippi River plume/Gulf shelf processes. p. 84-94. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

BETZER, P. R., W. J. SHOWERS, E. A. LAWS, C. D. WINN, G. D. DITULLIO, AND P. KROOPNICK. 1984. Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean. Deep-Sea Res. **31**: 1-11.

BHOSLE. N. B., S. S. SAWANT, P. D. SANKARAN, AND A. B. WAGH. 1989. Sedimentation of particulate material in stratified and nonstratified water columns in the Bombay High area of the Arabian Sea. Mar. Ecol. Prog. Ser. **57**: 225-236.

BIENFANG, P. K. 1980. Herbivore diet affects fecal pellet settling. Can. J. Fish. Aquat. Sci. **37**: 1352-1357.

BISHOP, J. K., J. M. EDMOND, D. R. KETTEN, M. P. BACON, AND W. B. SILKER. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. **23**: 511-548.

_____, R. W. COLLIER, D. R. KETTEN, AND J. M. EDMOND. 1980. The chemistry, biology and vertical flux of particulate matter from the upper 1500 m of Panama Basin. Deep-Sea Res. **27**: 615-640.

BLOMQVIST, S., AND U. LARSSON. 1994. Detrital bedrock elements as tracers of settling resuspended particulate matter in a coastal area of the Baltic Sea. Limnol. Oceanogr. **39**: 880-896.

BOCHDANSKY, A. B., AND G. J. HERNDL. 1992. Ecology of amorphous aggregations (marine snow) in the Northern Adriatic Sea. V. Role of fecal pellets in marine snow. Mar. Ecol. Prog. Ser. **89**: 297-303.

BURNS, K. A., J.-P. VILLENEUVE, AND S. W. FOWLER. 1985. Fluxes and residence times of hydrocarbons in the coastal Mediterranean: How important are the biota? Estuar. Coast. Shelf Sci. **20**: 313-330.

BUSCAIL, T., R. POCKLINGTON, R. DAUMAS, AND L. GUIDI. 1990. Fluxes and budget of organic matter in the benthic boundary layer on the northwestern Mediterranean margin. Cont. Shelf Res. **10**: 1089-1122.

DAGG, M. J., AND P. ORTNER. 1992. Mesozooplankton grazing and the fate of carbon in the northern Gulf of Mexico. p. 117-121. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, AND T. E. WHITLEDGE. 1991. Concentrations of copepod nauplii associated with the nutrient-rich plume of the Mississippi River. Cont. Shelf Res. **11**: 1409-1423.

DAVIES, J. M., AND R. PAYNE. 1984. Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. Mar. Biol. **78**: 315-324.

DEUSER, W. G., AND E. H. ROSS. 1980. Seasonal change in the flux of organic carbon to the deep Sargasso Sea. Nature **283**: 364-365.

_____, E. H. ROSS, AND R. F. ANDERSON. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. Deep-Sea Res. **28**: 495-505.

_____, P. G. BREWER, T. D. JICKELLS, AND R. F. COMMEAU. 1983. Biological contrl of the removal of abiogenic particles from the surface ocean. Science **219**: 388-391.

DILLING, L., AND A. L. ALLDREDGE. 1993. Can chaetognath fecal pellets contribute significantly to carbon flux? Mar. Ecol. Prog. Ser. **92**: 51-58.

DINNEL, S. P. 1993. Buoyancy and nutrient exchange in the Mississippi River outflow region. *In* S. E. Lohrenz [ed.], Proceedings of the 1993 NECOP Data Workshop. University of Southern Mississippi, Gulf Coast Campus, Long Beach, Mississippi (abstract).

DORTCH, Q. D. MILSTED, N. N. RABALAIS, S. E. LOHRENZ, D. G. REDALJE, M. J. DAGG, R. E. TURNER, AND T. E. WHITLEDGE. 1992. Role of silicate availability in phytoplankton species composition and the fate of carbon. p. 76-85. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

DORTCH, Q. 1994. Changes in phytoplankton numbers and species composition. p. 46-49. *In* M. J. Dowgiallo (ed.), Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding, Special NOAA Report, National Oceanic and Atmospheric Administration, Coastal Ocean Office, Silver Spring, Maryland.

DUNBAR, R. B., AND W. H. BERGER. 1981. Fecal pellet flux to modern bottom sediment of Santa Barbara Basin (California) based on sediment trapping. Geol. Soc. Am. Bull. **92**: 212-218.

EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature **282**: 677-680.

FAHNENSTIEL, G. L., M. MARCOVITZ, M. J. MCCORMICK, D. G. REDALJE, S. E. LOHRENZ, H. J. CARRICK, AND M. J. DAGG. 1992. High growth and microzooplankton-grazing loss rates for phytoplankton populations from the Mississippi River plume region. p. 111-116. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

FOWLER, S. W., S. BALLESTRA, J. LA. ROSA, AND R. FUKAI. 1983. Vertical transport of particulate-associated plutonium and americium in the northeast Pacific. Deep-Sea Res. **30**: 1221-1233.

GARDNER, W. D., AND M. J. RICHARDSON. 1994. IV. Sediment flux. p. 153-161. *In* S. P. Murray [ed.], Mississippi River Plume Hydrography: Annual Report. OCS Study/MMS 94-0028. U. S. Dept. of Interior, Minerals Management Service, Gulf of Mexico OCS Regional Office, New Orleans, Louisiana, 229 pp.

_____, K. R. HINGA, AND J. MARRA. 1983. Observations on the degradation of biogenic material in the deep ocean with implications on accuracy of sediment trap fluxes. J. Mar. Res. **41**: 195-214.

GARDNER, W. S., R, BENNER, G. CHIN-LEO, J. B. COTNER JR., B. J. EADIE, J. F. CAVETTO, AND M. B. LANSING. 1994. Mineralization of organic material and bacterial dynamics in Mississippi River plume waters. Estuaries **17**: in press.

HARDING, G. C., B. T. HARGRAVE, W. P. VASS, R. W. SHELDON, AND S. PEARRE, JR. 1987. Vertical flux of particulate matter by sedimentation and zooplankton movements in St. Georges Bay, the southern Gulf of St. Lawrence. Biol. Oceanogr. **4**: 323-357.

HARGRAVE, B. T., AND S.TAGUCHI. 1978. Origin of deposited material sedimented in a marine Bay. J. Fish. Res. Bd. Can. **35**: 1124-1136.

_____, G. A. PHILLIPS, AND S. TAGUCHI. 1976. Sedimentation measurements in Bedford Basin, 1973-1974. Tech. Rep. Fish. Mar. Serv. Can. **608**: 1-110.

HARVEY, H. W., L. H. N. COOPER, M. V. LEBOUR, AND F. S. RUSSELL. 1935. Plankton production and its control. J. Mar. biol. Ass. U. K. **20**: 407-441.

HEDGES, J. I., C. LEE, S. G. WAKEHAM, P. J. HERNES, AND M. L. PETERSON. 1993. Effects of poisons and preservatives on the fluxes and elemental compositions of sediment trap material. J. Mar. Res. **51**: 651-668.

HITCHCOCK, G. AND T. E. WHITLEDGE. 1992. Nutrient/pigment variability in the Mississippi River plume and adjacent waters. p. 43-51. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

HONJO, S. 1978. Sedimentation of materials in the Sargasso Sea at a 5,367 m deep station. J. Mar. Res. **36**: 469-492.

_____. 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. Mar. Res. **38**: 53-97.

_____. 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science **218**: 883-884.

_____, AND M. R. ROMAN. 1978. Marine copepod fecal pellets: production, preservation and sedimentation. J. Mar. Res. **36**: 45-57.

JUMARS, P. A., D. PENRY, J. A. BAROSS, M. J. PERRY, AND B. FROST. 1989. Closing the microbial loop: dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. Deep-Sea Res. **36**: 483-495.

JUSTIC', D., N. N. RABALAIS, R. E. TURNER, AND W. J. WISEMAN, JR. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. Mar. Pollut. Bull. **26**: 184-189.

KARL, D. M., AND G. A. KNAUER. 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence for multiple zones of biological activity. Deep-Sea Res. **31**: 221-243.

KNAUER, G. A., AND V. ASPER [EDS.]. 1989. Sediment trap technology and sampling. U. S. GOFS Planning Rep. 10.

_____, AND J. H. MARTIN. 1981. Primary production and carbon-nitrogen fluxes in the upper 1500 m of the northeast Pacific. Limnol. Oceanogr. **26**: 97-108.

_____, J. H. MARTIN, AND K. W. BRULAND. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res. **26**: 97-108.

_____, D. M. KARL, J.M. MARTIN, AND C. N. HUNTER. 1984. In situ effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. J. Mar. Res. **42**: 445-462.

LAMPITT, R. S., T. NOJI, AND R. VON BONUNGEN. 1990. What happens to zooplankton faecal pellets? Implications for material flux. Mar. Biol. **104**: 15-23.

LAWS, E. A., P. K. BIENFANG, D. A. ZIEMANN, AND L. D. CONQUEST. 1988. Phytoplankton population dynamics and the fate of production during the spring bloom in Auke Bay, Alaska. Limnol. Oceanogr. **33**: 57-65.

LEE, C., S. G. WAHEHAM, AND J. J. HEDGES. 1988. The measurement of oceanic particle flux- Are "swimmers" a problem? Oceanogr. Mag. **1**: 34-36.

_____, J. I.HEDGES, S. G. WAKEHAM, AND N. ZHU. 1992. Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnol. Oceanogr. **37**: 117-130.

LEGENDRE, L., AND J. LE FEVRE. 1989. Hydrodynamical singularities as controls of recycled versus export production in oceans, p. 49-63. *In* W. H. Berger, V. S. Smetacek, and G. Wefer [eds], Dahlem workshop reports: Productivity of the ocean: present and past. John Wiley & Sons.

LOHMANN, H. 1902. Die Coccolithophoridae, eine Monographie der Coccolithen bildenden Flagellaten, zugleich ein Beitrag zur Kenntnis des Mittelmeeratftriebs. Arch. Protistenka 1: 89-165.

LOHRENZ, S. E., M. J. DAGG, AND T. E. WHITLEDGE. 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Cont. Shelf Res. **10**: 639-664.

LORENZEN, C. J., N. A. WELSCHMEYER, A. E. COPPING, AND M. VERNET. 1983. Sinking rates of organic particles. Limnol. Oceanogr. **28**: 766-769.

MACEINA, M. J., P. W. BETTOLI, AND D. R. DEVRIES. 1994. Use of a split-plot analysis of variance design for repeated-measure fishery data. Fisheries. **19**: 14-20.

MADIN, L. P. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar. Biol. **67**: 39-45.

MARTIN, J. H., AND G. A. KNAUER. 1982. Manganese cycling in northeast Pacific equatorial waters. J. Mar. Res. **40**: 1212-1225.

_____, _____, D. M. KARL, AND W. W. BROENKOW. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res. **34**: 267-285.

MCCAVE, I. N. 1975. Vertical flux of particles in the ocean. Deep-Sea Res. **22**: 491-502.

MICHAELS, A. F., M. W. SILVER, M. M. GOWING, AND G. A. KNAUER. 1990. Cryptic zooplankton "swimmer" in upper ocean sediment traps. Deep-Sea Res. **37**: 1285-1296.

MIQUEL, J. C., S. W. FOWLER, .J. LA. ROSA, AND P. BAUT-MENARD. 1994. Dynamics of downward flux of particles and carbon in the open northwestern Mediterranean Sea. Deep-Sea Res. **41**: 243-265.

MONACO, A., P. BISCAYE, J. SOYER, R. POCKLINGTON, AND S. HEUSSNER. 1990a. Particle fluxes and ecosystem response on a continental margin: the 1985-1988 Mediterranean ECOMARGE experiment. Cont. Shelf Res. **10**: 809-839.

_____, T. COURP, S. HEUSSNER, J. CARBONNE, S. W. FOWLER, AND B. DENIAUX. 1990b. Seasonality and composition of particulate fluxes during ECOMARGE-I, western Gulf of Lions. Cont. Shelf Res. **10**: 959-987.

NOJI, T. T. 1991. The influence of macrozooplankton on vertical particulate flux. Sarsia **76**: 1-9.

ORTNER, P. B., L. C. HILL, AND S. R. CUMMINGS. 1989. Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. Cont. Shelf Res. **9**: 387-402.

PAFFENHOFER, G. A., AND S.C. KNOWLES. 1979. Ecological implications of fecal pellet size, production and consumption by copepods. J. Mar. Res. **37**: 35-49.

PETERSON, M. L., P. J. HERNES, D. S. THORESON, J. I. HEDGES, C. LEE, AND S. G. WAKEHAM. 1993. Field evaluation of a valved sediment trap. Limnol. Oceanogr. **38**: 1741-1761.

PILSKALN, C. H., AND S. HONJO. 1987. The fecal pellet fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles **1**: 31-48.

PUSKARIC, S., S. W. FOWLER, AND J. CA. MIQUEL. 1992. Temporal changes in particulate flux in the northern Adriatic Sea. Estuarine, Coast. Shelf Sci. **35**: 267-287.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR. AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988, p. 35-47. *In* R. V. Tyson, and T. H. Pearson [eds.], *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication No. 58, The Geological Society, London.

_____, _____, AND _____. 1992. Distribution and characteristics of hypoxia on the Louisiana shelf in 1990 and 1991. p. 15-20. *In* Proceedings, NECOP Synthesis Meeting, Publ. NO. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, _____, AND _____. 1994a. Hypoxia conditions in bottom waters on the Louisiana-Texas shelf. Pages 50-54 *In* M. J. Dowgiallo (ed.), Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding, Special NOAA Report, National Oceanic and Atmospheric Administration, Coastal Ocean Office, Silver Spring, Maryland.

_____, W. J. WISEMAN, JR., AND R. E. TURNER. 1994b. Comparison of continuous records of near bottom dissolved oxygen from the hypoxic zone of Louisiana. Estuaries **17**: 850-861.

REDALJE, D. G., S. E. LOHRENZ, AND G. L. FAHNENSTIEL. 1992. The relationship between primary production and export of POM from the photic zone in the Mississippi River plume and inner Gulf of Mexico shelf region. p. 105-110. *In* Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, _____, AND _____. 1994. The relationship between primary production and the vertical export of particulate organic matter in a river impacted coastal ecosystem. Estuaries **17**: in press.

RIEBESELL, U. 1989. Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom. Mar. Ecol. Prog. Ser. **54**: 109-119.

SAS INSTITUTE. 1985. SAS User's Guide: Statistics, Version 5 edition. SAS Institute Inc., North Carolina, 956 p.

SHANKS, A. L., AND J. D. TRENT. 1980. Marine snow: sinking rates and potential role in vertical flux. Deep-Sea Res. **27**: 137-143.

SILVER, M. W., AND A. L. ALLDREDGE. 1981. Bathypelagic marine snow: deep-sea and detrital community. J. Mar. Res. **39**: 501-530.

SKJOLDAL, H. R., AND P. WASSMANN. 1986. Sedimentation of particulate organic matter and silicium during spring and summer in Lindaspollene, Western Norway. Mar. Ecol. Prog. Ser. **30**: 49-63.

SKLAR, F. H. 1976. Primary productivity in the Mississippi delta bight near a shallow bay estuarine system in Louisiana. M. S. Thesis, Louisiana State University, Baton Rouge.

_____, AND R. E. TURNER. 1981. Plankton production in Louisiana coastal zone as influenced by the Mississippi River. Contrib. Mar. Sci. **24**: 93-106.

SMETACEK, V. S. 1980. Zooplankton standing stock, copepod fecal pellets and particulate detritus in Kiel Bight. Estuar. Coast. Mar. Sci. **11**: 470-490.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and Procedures of Statistics. McGraw Hill, New York.

STOECKER, D. K. 1984. Particle production by planktonic ciliates. Limnol. Oceanogr. **29**: 930-940.

SUESS, E. 1980. Particulate organic carbon flux in the ocean -- surface productivity and oxygen utilization. Nature **288**: 260-263.

TURNER, J. T., AND J. G. FERRANTE. 1979. Zooplankton fecal pellets in aquatic ecosystems. BioScience **29**: 670-675.

TURNER, R. E., AND N. N. RABALAIS. 1991. Changes in Mississippi River water quality this century and implications for coastal food webs. BioScience **41**: 140-147.

_____, AND _____. 1994. Coastal eutrophication near the Mississippi river delta. Nature **368**: 619-621.

_____, R. E., R. KASWADJI, N. N. RABALAIS, AND D. F. BOESCH. 1987. Long-term changes in the Mississippi River water quality and its relationship to hypoxic continental shelf waters. p. 261-266. *In* Estuarine and Coastal Management. Proceedings of the 10th National Conference of the Coastal Society 12-15 October, 1986, New Orleans, Louisiana.

URRERE, M. A., AND G. A. KNAUER. 1981. Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. J. Plankton Res. **3**: 369-387.

WAKEHAM, S. G., J. I. HEDGES, C. LEE, AND T. K. PEASE. 1993. Effects of poisons and preservatives on the composition of organic matter in a sediment trap experiment. J Mar. Res. **51**: 669-696.

WALSH, J. J., D. A. DIETERLE, M. B. MEYERS, AND F. E. MULLER-KARGER. 1989. Nitrogen exchange at the continental margin: a numerical study of the Gulf of Mexico. Prog. Oceanogr. **23**: 245-301.

WASSAMANN, P. 1983. Sedimentation of organic and inorganic particulate material in Lindaspollene, a stratified, land-locked fjord in western Norway. Mar. Ecol. Prog. Ser. **13**: 237-248.

WELSCHMEYER, N. A., A. E. COPPING, M. VERNET, AND C. J. LORENZEN. 1984. Diel fluctuation in zooplankton grazing rate as determined from the downward vertical flux of phaeopigments. Mar. Biol. **83**: 263-270.

WIEBE, P. H., S. H. BOYD, AND C. WINGET. 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean, Bahamas, with a description of a new sedimentation trap. J. Mar. Res. **34**: 341-354.

CHAPTER 4

MESOZOOPLANKTON IN THE SURFACE WATERS OF A RIVERINE-INFLUENCED CONTINENTAL SHELF

INTRODUCTION

Freshwater inflow and nutrient flux to the Louisiana and Texas continental shelf is dominated by the Mississippi-Atchafalaya River system. Peak runoff occurs in spring (March - May) and low flow occurs in summer-fall (July - November) (Dinnel & Wiseman 1986). Inter-annual variability in the magnitude and the timing of flow can be high. There is a seasonal signal in nutrient flux to the adjacent shelf (Turner & Rabalais 1991, Dinnel & Bratkovich 1993), as well as long-term trends in the annual and seasonal nutrient concentrations, ratios and fluxes (Turner & Rabalais 1991, 1994, Justic' et al. 1994).

The influence of the Mississippi-Atchafalaya riverine inputs is seen in stratified, highly productive coastal waters. High nutrient concentrations are correlated with high chlorophyll *a* biomass and high primary productivity (Riley 1937, Sklar & Turner 1981, Lohrenz et al. 1990, Turner & Rabalais 1994). High chlorophyll *a* biomass is typical of Gulf of Mexico waters close to the Mississippi River delta, but with great seasonal variability (200-3000 mg m^{-3}) (Bogdanov et al. 1969). Correspondence between chlorophyll *a* and high copepod naupliar abundance has been observed (Dagg et al. 1987). The significance and importance of this to the marine ecosystem, in general, and larval recruitment of commercial species, specifically, is well recognized (Shaw et al. 1985, Govoni et al. 1989, Ortner et al. 1989). Local conditions, such as winds and currents, affect the distribution of river runoff, with subsequent variation in the composition and abundance of plankton that can be observed from year to year. In addition, physical stratification of coastal and nearshore waters provides a mechanism

for the establishment of high concentrations of zooplankton, by providing an environment in which prey aggregation can occur (Dagg et al. 1987).

Zooplankton quantitatively and qualitatively enhance sedimentation by producing fecal pellets with faster sinking rates (Madin 1982) than phytoplankton cells and are a major vehicle of transport of carbon to the seafloor (McCave 1975, Turner & Ferrante 1979, Noji 1991). Zooplankton, on the other hand, are also responsible for recycling of pelagic organic material by grazing, remineralizing and fragmenting fecal pellets (Lampitt et al. 1990, Noji 1991). Zooplankton can, furthermore, influence sedimentation by selective and discriminant feeding of particles (Haberyan 1985, Noji 1991), and by migration, or 'biological pumping', which can also affect and enhance sedimentation to the seafloor (Walsh et al. 1988, Dagg & Walser 1987, Longhurst & Harrison 1988).

Organic loading to the bottom, by phytoplankton cells or by larger particles, fecal pellets and aggregates, along with a stratified and stable water column contributes to the episodes of hypoxia observed during summer on the inner continental shelf of the northern Gulf of Mexico (Rabalais et al. 1991). Respiration rates, combined water column and sediment, are sufficient to deplete the bottom water oxygen within days to months, depending on the season and location (Turner & Allen 1982, Dortch et al. 1994). The contribution of fecal pellets to the total organic material flux to the sea floor varies from 1% to 90% (Pilskaln & Honjo 1987, Bathmann et al. 1987, Chapter 3), and is a function of seasonal surface productivity, zooplankton community structure and grazing activity of meso- and microzooplankton.

I have determined that the export of carbon from surface waters to the lower water column and sediments on the southeastern Louisiana shelf under the influence of the Mississippi River is high (Chapter 3). Further, the flux of carbon via fecal pellets averages 55% of the total particulate carbon flux from surface waters to the lower water column. This study was designed to identify the mesozooplankton inhabiting the study

area and to identify potential source organisms that were producing the fecal pellets collected in the sediment traps.

The objectives of this study were to (1) determine the surface water mesozooplankton community structure, (2) determine the copepod species composition, and (3) determine the seasonal variation in the mesozooplankton community. The samples were taken in the vicinity of the moored sediment traps. The composition of the mesozooplankton community was examined in relationship to environmental variables to identify the most important features of the system that determine seasonal patterns. Knowledge of the mesozooplankton community composition should provide insight to the potential sources of fecal pellets collected in the moored sediment traps (Chapters 2 and 3).

METHODS

Mesozooplankton samples were collected at monthly intervals from May to September 1992. Five minute surface tows were made with a standard plankton net (mouth diameter of 0.5 m and 234 μm mesh) to collect mesozooplankton (> 200 μm) in the vicinity of an instrument mooring at station C6B (28°50.41'N, 90°26.03'W). The instrument mooring included sediment traps from which materials were analyzed for fecal pellet number and carbon flux (Chapters 2 and 3). Flowmeter readings were recorded for each tow. The sample was concentrated and stored in 4% buffered formalin pending laboratory processing. Ancillary data included salinity, temperature, dissolved oxygen, nutrients and chlorophyll *a* and phaeopigment concentrations.

In 1991 zooplankton samples were collected using a smaller standard net (0.3 m mouth diameter, 200 μm mesh) without a flowmeter from July through September. The 1991 samples provided qualitative information of the zooplankton community structure for comparison to 1992.

Zooplankton samples were subsampled by adding water to bring the samples to a known volume (500 or 1000 ml). Each sample was then agitated and dispersed evenly. If the sample was very dense, it was split in a Folsom plankton splitter. An aliquot of 2 ml was collected from the sample or subsample (i. e., split) by Stemple pipette and placed in a counting wheel for identification and enumeration of organisms. Three to four replicate subsamples were examined and were averaged. Mesozooplankton were identified to the lowest possible taxon (order, planktonic form, family, genus). Copepods were more abundant and were identified to species. Larval stages of copepods (nauplii and copepodites when present) were also recorded. Flow meter readings were used to calculate abundance (no. m^{-3}), assuming 100% filtering efficiency.

In order to characterize zooplankton and copepod communities, the Shannon-Wiener diversity index (H) (Shannon & Weaver 1963) and the equitability index (J) (Pielou 1969) were used:

$$H = -\Sigma_{i=1\text{-}s} (p_i) (\log_{10} p_i) \qquad \text{Equation 4.1}$$

where p_i is the proportion of total sample belonging to ith species, and i is equal to 1 to s number of species. Equitability can be measured in several ways. The simplest is:

$$H_{max} = \log_{10} S \qquad \text{Equation 4.2}$$

where H_{max} is equal to species diversity under conditions of maximal equitability or maximum species diversity, S is number of species in the community. Equitability (J) (range 0-1) is defined as:

$$J = H/H_{max} \qquad \text{Equation 4.3}$$

RESULTS

The average total mesozooplankton abundance in 1991 was 179 sample^{-1} (non-quantitative sampling) and was 9353 m^{-3} in 1992 with the highest number in June 1992 (41,529 m^{-3}) and the lowest number in July 1992 (843 m^{-3}) (Table 4.1). The abundance of mesozooplankton increased in August and September (Fig. 4.1).

Copepods were the dominant mesozooplankters, contributing 60% of the total mesozooplankton in 1991 (an average of 106 m^{-3}) and 50% of the total mesozooplankton in 1992 (an average of 4352 m^{-3}) (Table 4.1). Exceptions were August 1991 and July 1992, when percent copepods were the lowest (23% and 12%, respectively) and the larvaceans (*Oikopleura*) were the dominant organisms (Fig. 4.2). Other zooplankton groups that alternated in dominance after copepods included larvaceans, doliolids, chaetognaths, decapod larvae and meroplankton (larvae of polychaetes and brittle stars, and juveniles of brittle stars) (Fig. 4.2).

The percentage of copepods in 1991 was high in July, lower in August and increased in September (Figs. 4.2 and 4.3). The percentage of copepods in 1992 was high in May, was the lowest in July, corresponding to the low total mesozoooplankton abundance, and increased from August through September (Figs. 4.2, 4.4 - 4.5). Fourteen species of copepods were identified, representing three orders (calanoids, cyclopoids and harpacticoids). Calanoids were the dominant copepods, with *Acartia tonsa* and *Paracalanus* sp. being the most abundant, followed by *Labidocera scotti, Centropages furcatus.* Among the cyclopoids, *Temora turbinata* and *Corycaeus clausi* alternated in abundance (Figs. 4.6 - 4.8).

The population parameters of the mesozooplankton community and copepods, diversity and evenness, are given in Table 4.1. The Shannon-Wiener diversity index was low in both years (average of 0.40 and 0.56, respectively, for 1991 and 1992), with

Table 4.1. Mesozooplankton and copepod abundance, percent copepod of the total (%), diversity (Shannon-Wiener Index) and equitability for samples collected near station C6B during 1991 and 1992.

Date	Mesozooplankton Abundance	Mesozooplankton Diversity (H)	Mesozooplankton Equitability (J)	Copepod Abundance	Percent Copepod (%)	Copepod Diversity (H)	Copepod Equitability (J)
1991	no./sample			no./sample			
7.09.91	77	0.41	0.44	60	78	0.61	0.72
8.13.91	186	0.39	0.32	45	23	0.56	0.68
9.17.91	275	0.40	0.44	214	78	0.40	0.52
Mean	179	0.40	0.40	106	60	0.52	0.64
1992	no./m^3			no./m^3			
5.26.92	1172	0.49	0.47	806	70	0.73	0.77
6.17.92	41529	0.71	0.59	17327	42	0.51	0.51
7.20.92	843	0.53	0.46	103	12	0.65	0.77
8.01.92	2212	0.82	0.74	866	41	0.58	0.68
8.12.92	5135	0.46	0.44	2779	55	0.55	0.70
9.18.92	5228	0.34	0.28	4229	81	0.53	0.47
Mean	9353	0.56	0.50	4352	50	0.59	0.65

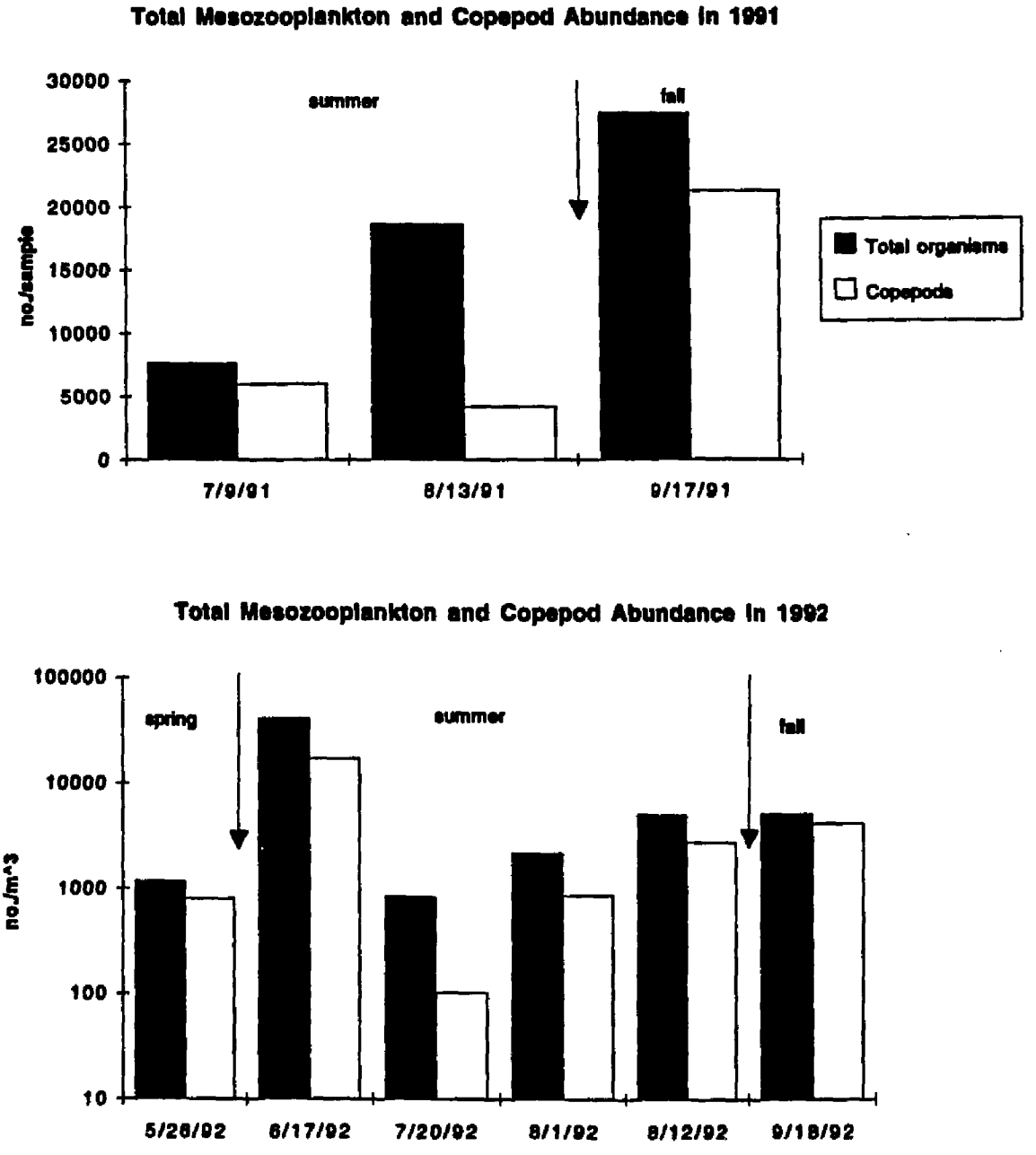


Figure 4.1. Abundances of mesozooplankton and copepods (no. sample^{-1} and no. m^{-3}, respectively, in 1991 and 1992) in the vicinity of station C6B. Arrows delineate seasons corresponding to the sediment trap data (Chapter 2).

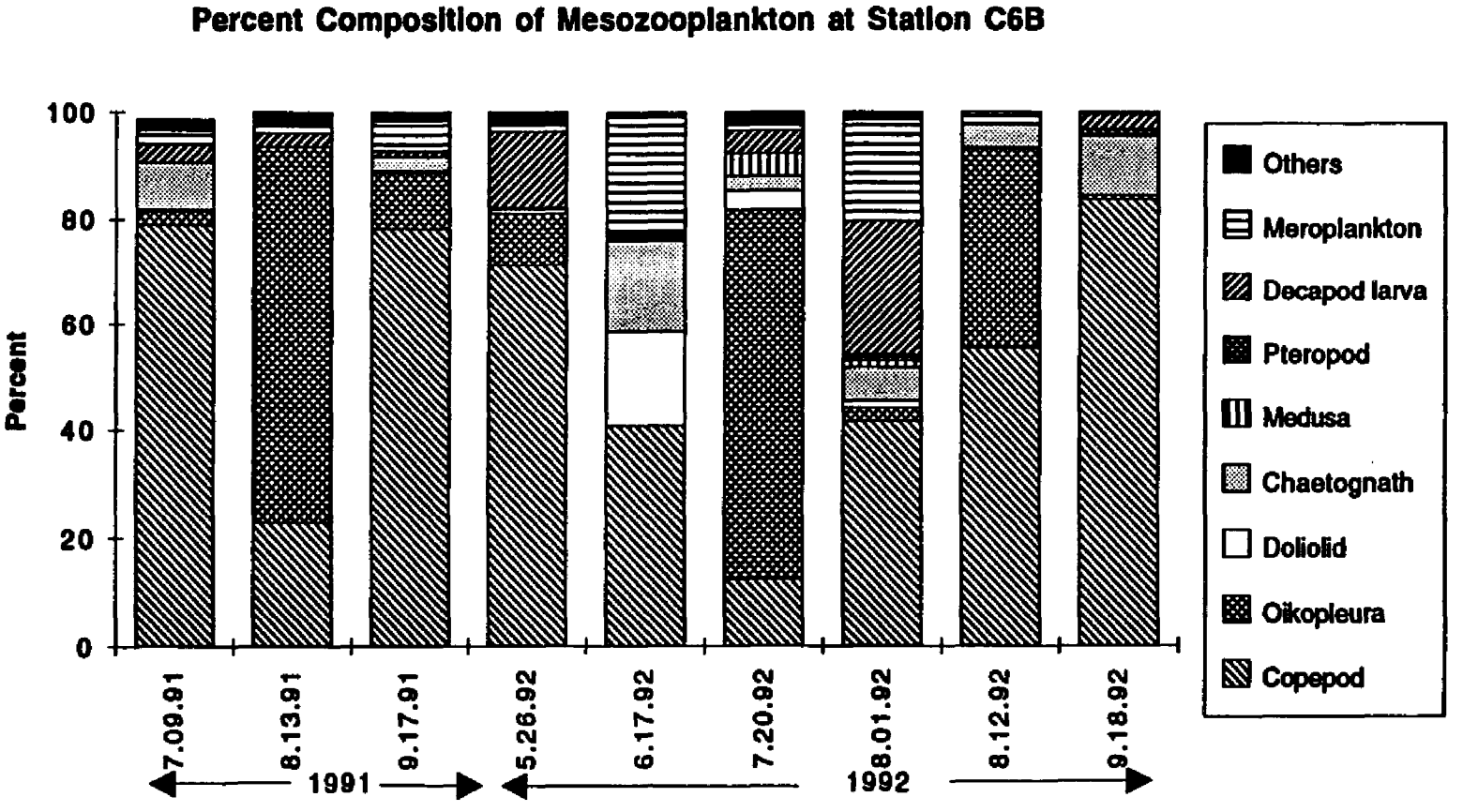


Figure 4.2. Percent composition of the mesozooplankton community in the vicinity of station C6B during 1991 and 1992.

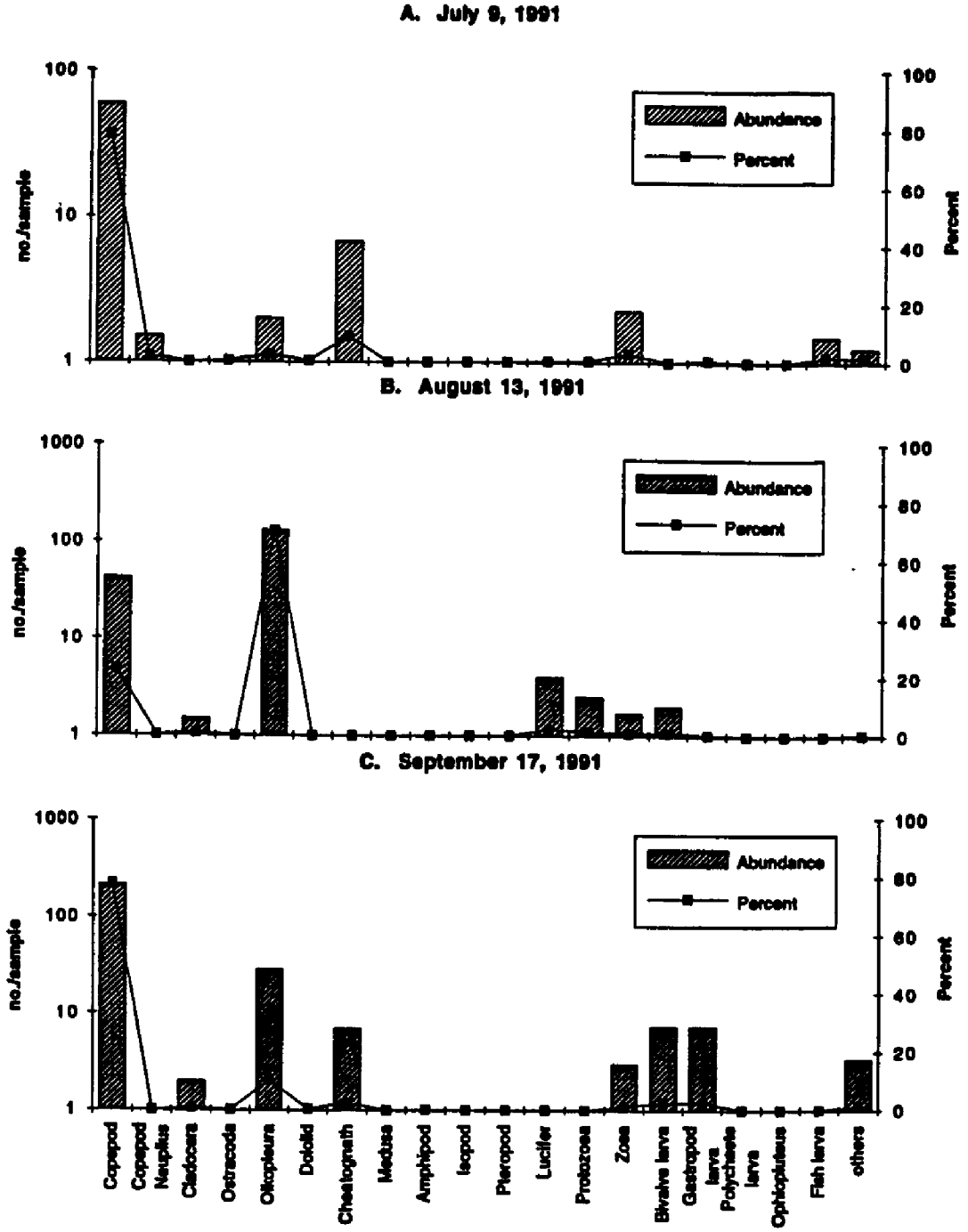


Figure 4.3. Abundance (no. sample^{-1}) and percent composition of mesozooplankton community at station C6B during July - September 1991.

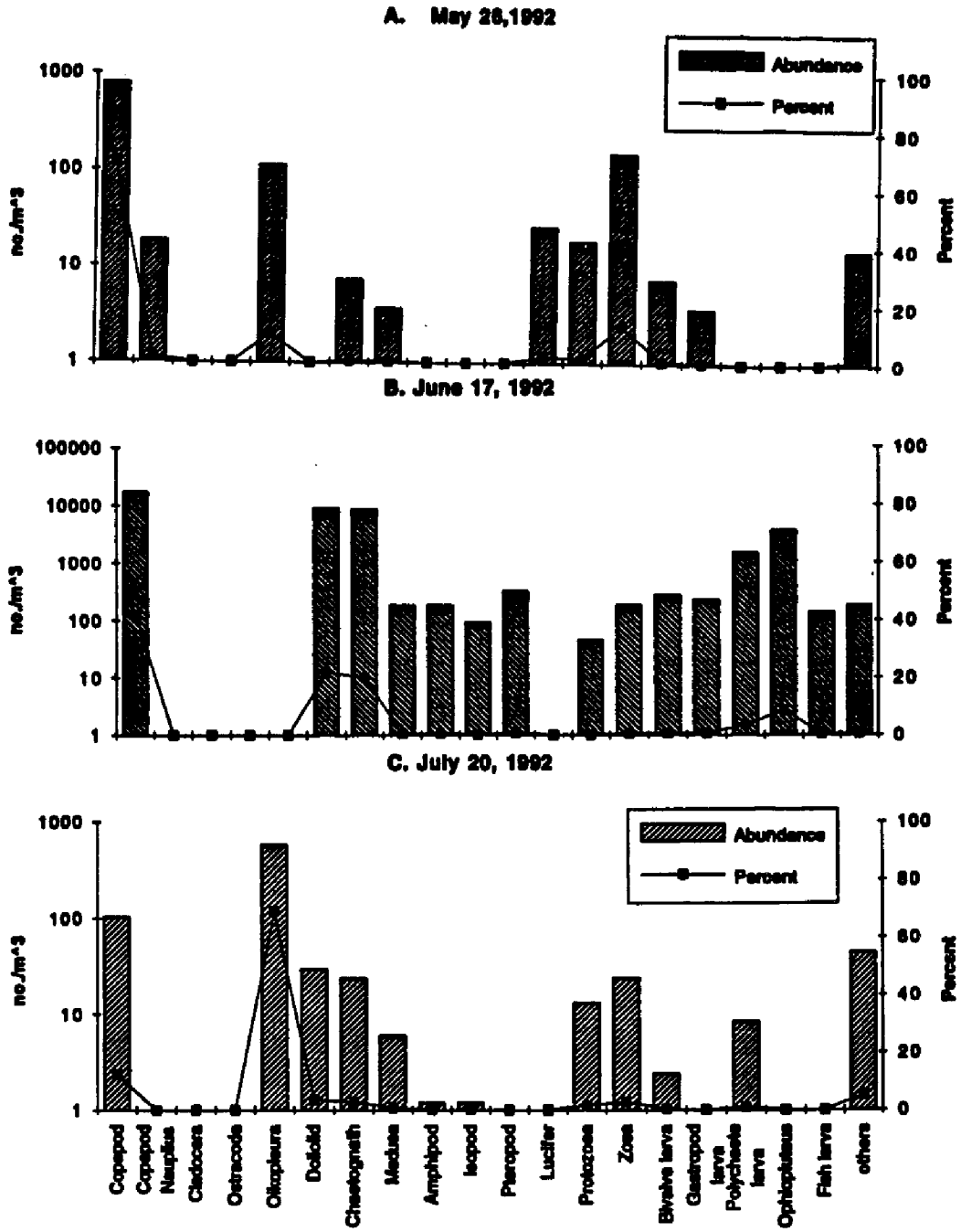


Figure 4.4. Abundance (no. m^{-3}) and percent composition of mesozooplankton community at station C6B during May - July 1992.

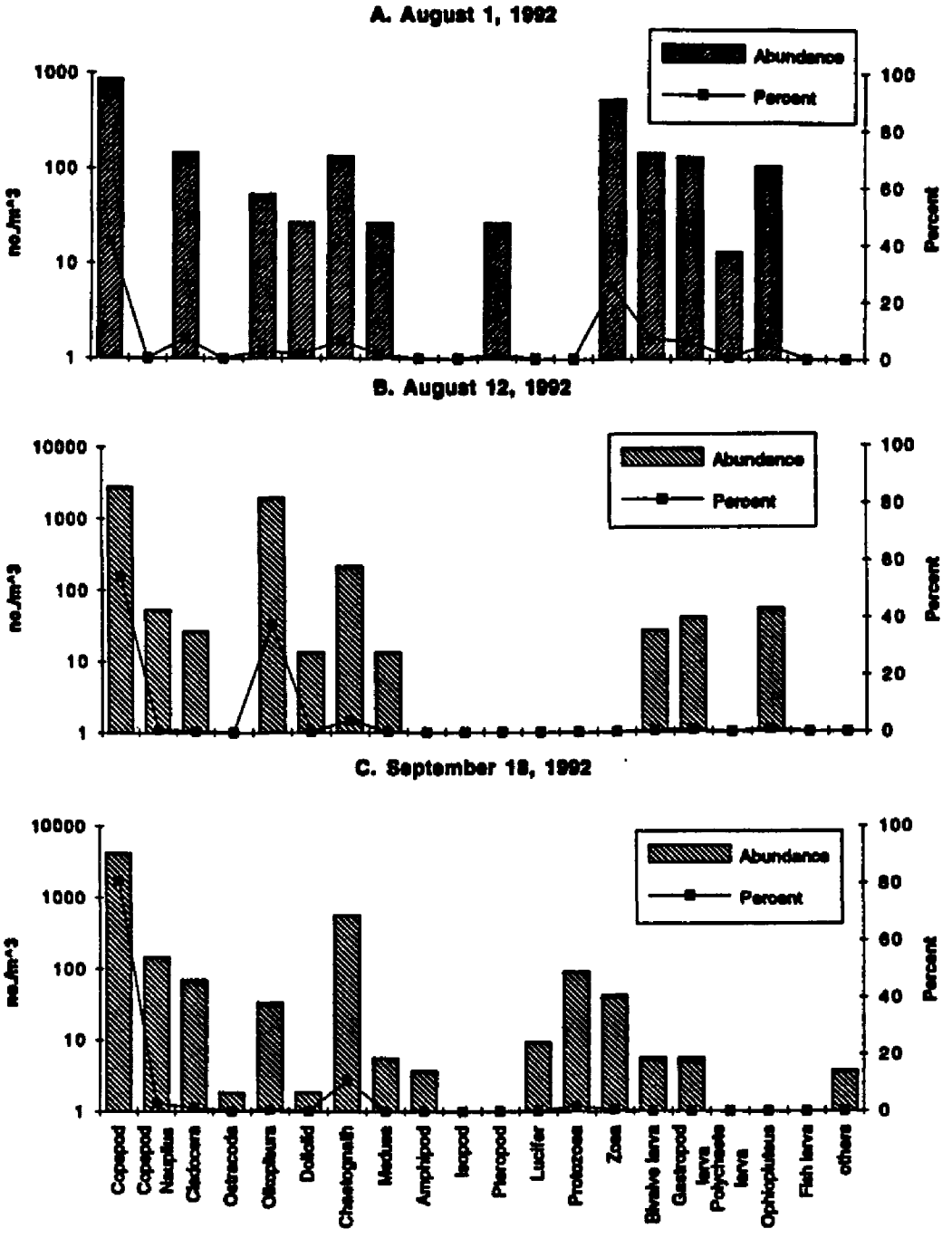


Figure 4.5. Abundance (no. m^{-3}) and percent composition of mesozooplankton community at station C6B during August - September 1992.

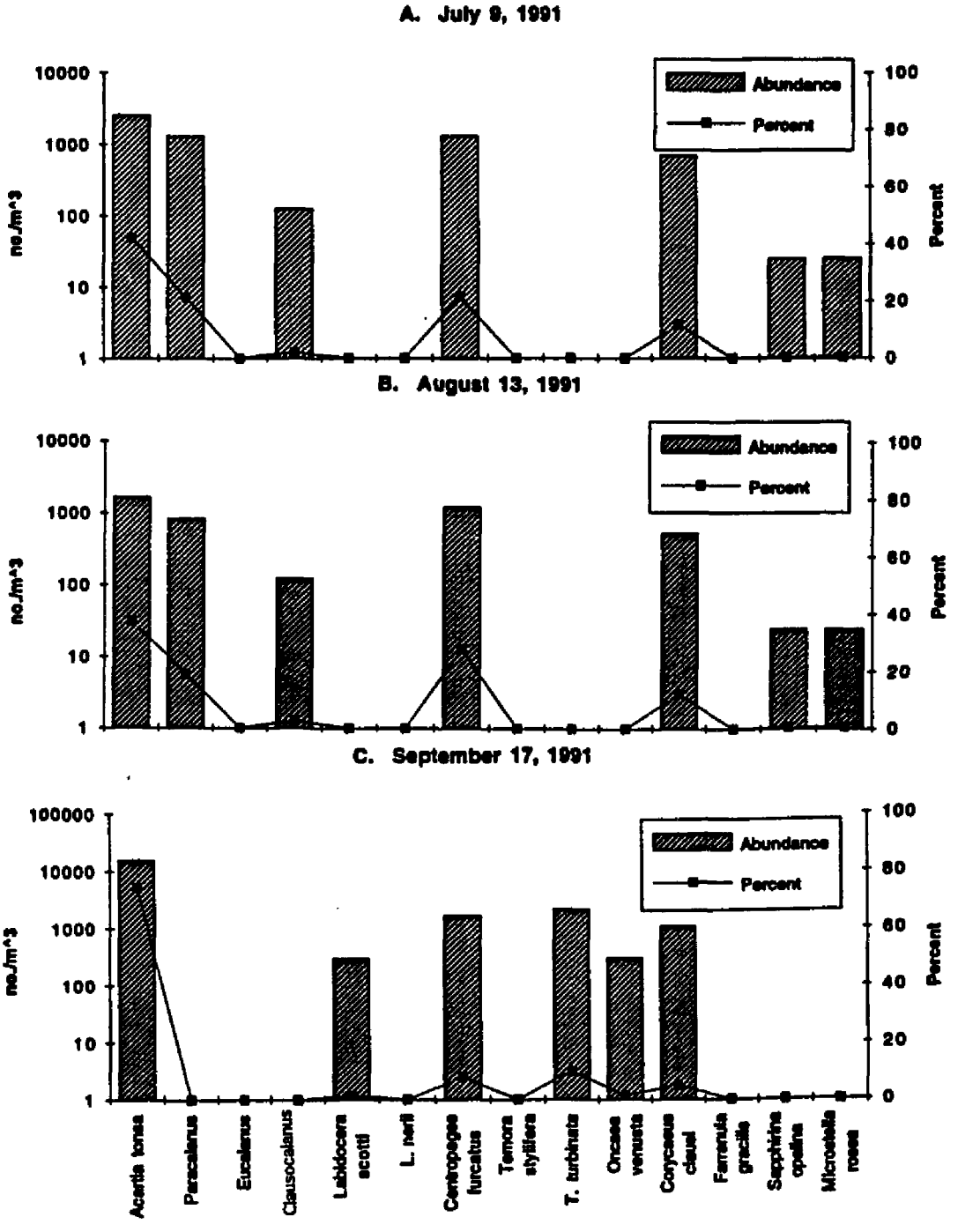


Figure 4.6. Abundance (no. sample^{-1}) and percent composition of copepods at station C6B during July - September 1991.

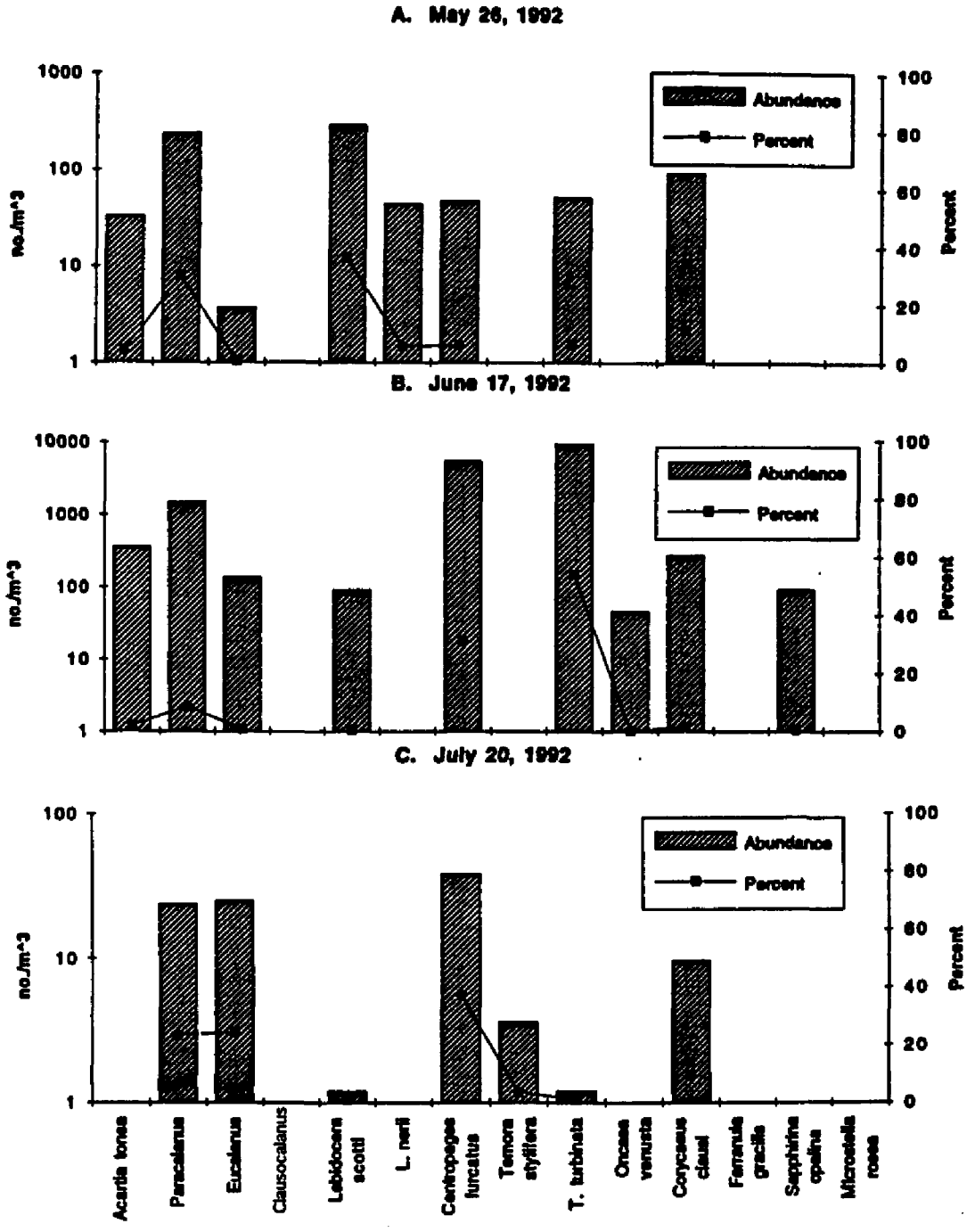


Figure 4.7. Abundance (no. m^{-3}) and percent composition of copepods at station C6B during May - July 1992.

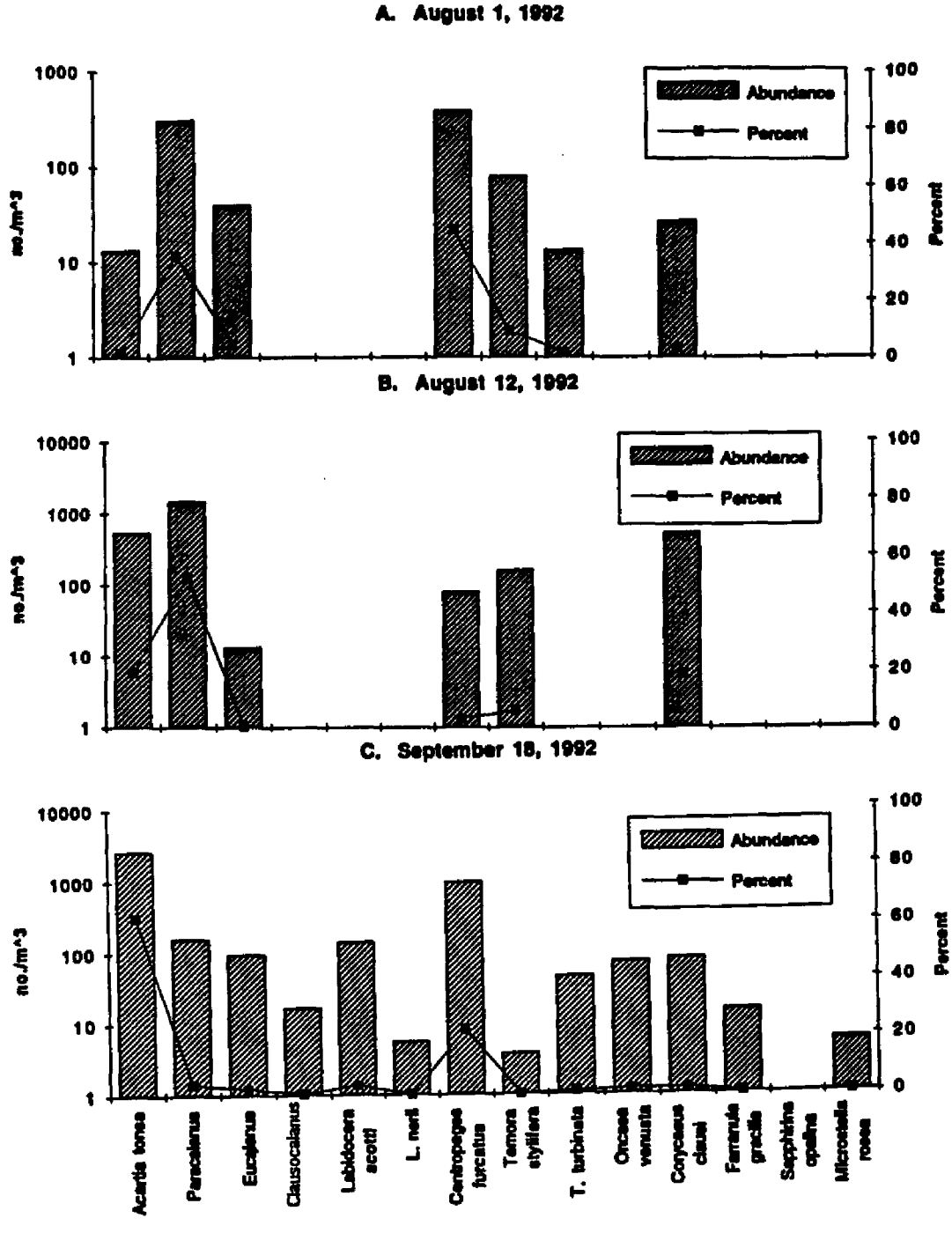


Figure 4.8. Abundance (no. m^{-3}) and percent composition of copepods at station C6B during August - September 1992.

low equitability (average of 0.40 and 0.50, respectively, for 1991 and 1992) (Table 4.1). The highest diversity in early August 1992 (0.82) corresponded to a high evenness (0.74), and the lowest diversity (0.34) in September 1992 corresponded to the lowest evenness (0.28) (Table 4.1). Copepod diversity values were similar to the overall mesozooplankton community diversity. The average diversity index for copepods species was lowest in September 1991 (0.40) and was highest in May 1992 (0.73). The copepods were fairly evenly distributed in both years (average equitability of 0.64 and 0.65, respectively, for 1991 and 1992); and were the lowest in September 1992 (Table 4.1).

Station C6B is influenced by the effluents of the Mississippi River and surface salinities are frequently less than 30 ppt. Abundances of mesozooplankton were strongly and negatively related with surface water salinity, when the June data were excluded from the comparison ($r^2 = 0.78$), which indicated that higher mesozooplankton abundances occurred at lower salinities (Fig. 4.9). The correlations between zooplankton abundance and copepod abundance with chlorophyll *a* and phaeopigments were very weak (not significant and low r^2). Copepod abundance was negatively related to salinity (very weak relationship with June data included, $r^2 = 0.09$). Copepod dominance of the community was indicated by a strong positive correlation between mesozooplankton and copepods ($r^2 = 0.78$) (Fig. 4.10).

DISCUSSION

Data Limitations

The ability to describe zooplankton communities is biased by the sampling program and the equipment. Another bias is the inherent assumption of an even distribution of the subsampled population, which is rare, because of the patchy distribution of zooplankton. Differences in abundance at fine (few meters) to coarse

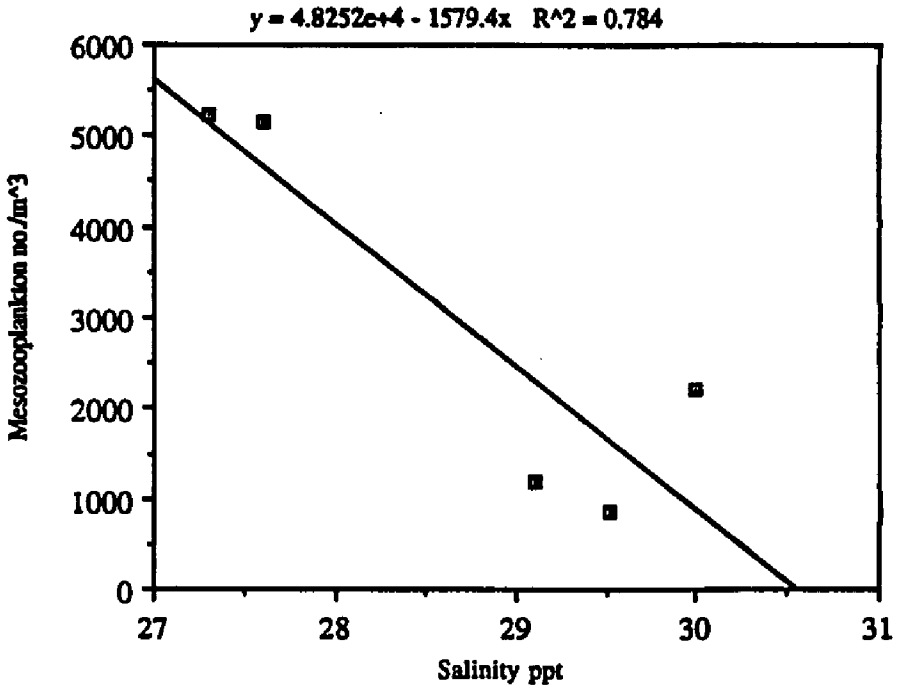


Figure 4.9. Relationship between total mesozooplankton (no. m^{-3}) and surface water salinity (ppt) at station C6B during 1992.

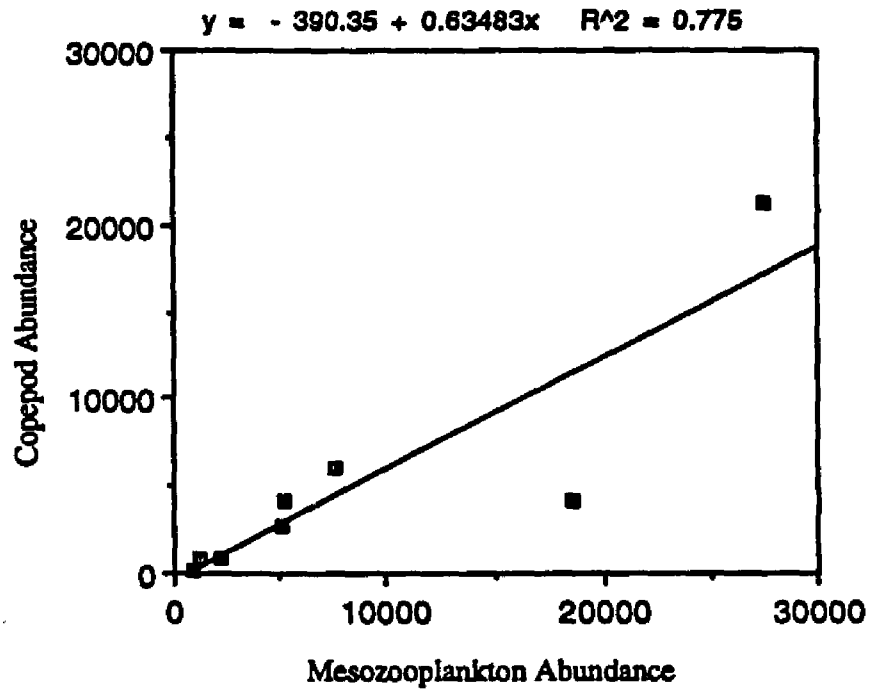


Figure 4.10. Relationship between total mesozooplankton and copepod abundances (no. m-3) at station C6B during 1992.

scales (10 - 100 km) have been reported (Longhurst 1981, Wiebe 1970, Govoni et al. 1989). Embedded in this spatial distribution is variability due to diel vertical migration

Samples in this study were collected from the surface waters at a single station, near the instrument mooring and, thus, represent a limited horizontal and vertical scale. The temporal scale was also limited in both monthly frequency and duration within either year. Samples were collected for part of the year and did not cover the whole period corresponding to the sediment traps. The mesozooplankton samples were sufficient, however, to describe what was present at the times sampled and were useful in identifying dominant zooplankters which were potentially responsible for fecal pellets produced in the area and collected in the sediment trap samples. The mesozooplankton collected near the instrument mooring very likely represent a portion of the community contributing to the fecal pellet flux.

Temporal Variability

There were monthly differences in the mesozooplankton community and abundances of organisms but no clear seasonal trends, possibly because of the limited number of samples and short duration of the study. Overall, most zooplankton abundances ranged between 10^3 and 10^4 m^{-3}. The highest abundances occurred in June 1992, well over 10^5 m^{-3}. Copepod abundances were more variable, ranging between 10^2 and 10^5 m^{-3}, but following the same pattern as the total abundances.

Temporal variations and seasonality in the abundance of zooplankton and copepods have been observed for both coastal and oceanic waters in the Gulf of Mexico (Fleminger 1956, Houde & Chitty 1976). Increased concentrations of microzooplankton (copepod nauplii) have been observed within the frontal regions of Mississippi plume where nutrient-rich turbid water, mixed with nutrient-depleted non turbid water, enhances primary productivity (Dagg & Whitledge 1991). Some of these variations seen in the zooplankton were possibly due to year-to-year variability in

environmental factors related to the flow of the Mississippi River. There was a negative relationship between zooplankton abundances and salinity ($r^2 = -0.78$) (zooplankton abundance in June 1992 was very high and was not included in the calculations). Most of the water leaving the Mississippi River through Southwest Pass courses in a westerly direction (Dinnel & Wiseman 1986). The study site near the mooring is directly under the influence of this discharge. The Mississippi river discharge, with its high nutrient load, plays an important part in stimulating primary production and in ultimately sustaining high zooplankton biomass and abundance in near-surface samples (Dagg et al. 1987, Dagg & Whitledge 1991, Ortner et al. 1989, Govoni et al. 1989). Nutrients and chlorophyll *a* concentrations were high in the surface waters in May 1992 (Chaper 2). This was possibly responsible for the high zooplankton abundance in the next month (June) (Fig. 4.1).

The relationship between surface chlorophyll *a* concentration with zooplankton abundance has been difficult to establish (Dagg et al. 1987, Dagg & Whitledge 1991, Pieper et al. 1990), but a weak relationship between naupliar abundance and chlorophyll concentrations in the Mississippi outflow region was observed by Dagg et al. (1987). The correlations between zooplankton abundance and copepod abundance with chlorophyll *a* and phaeopigments were very weak in this study. Dagg and Whitledge (1991) found no relationship between naupliar concentration and chlorophyll *a* concentration in the Mississippi plume area, and suggested a complex link between phytoplankton production and grazing transfer, attributable to greater trophodynamic complexity. Roman et al. (1986) also found no relationship between zooplankton abundance and phytoplankton biomass, however, they did find zooplankton biomass and grazing maxima generally occurred at the depth of the highest primary production.

The mid-summer low zooplankton abundances, especially in copepods, suggest the possible control of zooplankton by predation and or by food limitation (Villate 1991). It has been also suggested that an enhanced food environment, evident by high

zooplankton biomass in the mixed water near the Mississippi River plume, allows for the enhanced survival and growth for fish larvae (Shaw et al. 1985, Dagg et al. 1987, Govoni et al. 1989). The high zooplankton biomass would support high ichthyoplankton concentrations, and microzooplankton, including copepod nauplii and copepodites, are known to be an important component of larval fish diets (Govoni & Chester 1990). Elevated predation by fish larvae and zooplankton will terminate high secondary and primary production. If nutrient resupply is not continued, this would also create a food limitation in summer. This predation pressure not only controls the abundance of zooplankton but can also change the composition and size spectrum of the zooplankton community (Villate 1991).

Copepods were the dominant mesozooplankters (Fig. 4.1) comprising 50 - 60% of the total mesozooplankton (Table 4.1). Copepods composed up to 87% of the zooplankton in the nearshore region of the Mississippi River outflow (Ortner et al. 1989). The dominant copepod species at station C6B were *Acartia tonsa, Paracalanus* sp., *Temora turbinata, Centropages furcatus* and *Labidocera scotti*. These species are characteristic coastal, less saline water species. Other species observed, like *Classocalanus* sp., *Oncaea venusta, and Corycaeus clausii*, are transition water species found at higher salinities (Ortner et al. 1989).

Population parameters are valuable tools in characterizing zooplankton communities (Howey 1976). Low diversity indices for the mesozooplankton community, as well as the copepods, were comparable to the low diversity observed at the Mississippi outflow region (Ortner et al. 1989). Ortner et al. (1989) found that diversity indices, based on functional groups, represented a gradient of low diversity in the Mississippi outflow, to intermediate diversity at Cape San Blas, and high diversity in the central Gulf. The number of types found did not vary greatly, and the gradient in diversity index from the central Gulf of Mexico to the Mississippi River outflow region was due to a change in evenness of the distribution (Ortner et al. 1989).

Mesozooplankton Grazing Potential

Grazing by zooplankton is an important factor that regulates phytoplankton biomass. Dagg and Ortner (1992) measured the grazing pressure of mesozooplankton by extrapolating individual grazing rates of important copepod species to community grazing rates coupled with abundance and distribution data from the plume region and the hypoxic region in July 1990. The copepod community grazed an average of 17.8% of the primary production in the plume area, where ingestion and primary production both were higher compared to, an average of 14%, on the shelf in the hypoxic region (Dagg & Ortner 1992). They suggested an immediate initial fate of enhanced phytoplankton production in July 1990 was to be grazed by the copepod community in both the plume and the hypoxic regions. I estimated that fecal pellet carbon accounted for 55% of the total particulate organic matter flux from surface waters to the lower water column (Chapter 3). I also estimated much higher percentages of integrated primary production to be fluxed via fecal pellets (40% at 5-6 m and 25% at 15 m) (Chapter 3).

Copepods comprised a large percentage of the total mesozooplankton in this study but were lower than others (87%) reported from the same region (Hopkins 1982, Ortner et al. 1989, Dagg & Ortner 1992). There were temporal shifts in the dominants of the mesozooplankton community. Low abundances of copepods in summer were usually replaced by larvaceans (*Oikopleura*). Both taxa were present in significant enough numbers to exert high grazing pressure on the phytoplankton community (Dagg & Ortner 1992, M. Dagg pers. comm.). Mesozooplankton grazers produce larger fecal pellets, and these fecal pellets sink rapidly to the bottom and thus contribute to the flux of organic material.

Fecal pellet flux into the moored sediment traps was higher in the spring and fall compared to the summer (Chapter 2). The mesozooplankton abundances did not follow this same general trend, but surface water zooplankton samples were not taken at the

same regularity or frequency as the sediment trap samples. The meso- and microzooplankton samples collected at discrete depths on a monthly schedule during 1992 from March - September, however, did exhibit the same seasonal trends as the fecal pellet flux data for 1992 (Chapter 5 cf. Chapter 2). The discrete depth sampling design represented the whole water column, whereas the surface zooplankton tows sampled only a small percentage of the zooplankton community. A large proportion of the zooplankton community resided in the lower water column (Chapter 5), and the surface mesozooplankton collections enumerated the part of the water column where the lowest proportions resided (Chapter 5).

The high coherence among total organisms, copepods, copepod nauplii and fecal pellet abundances in the discrete depth sampling study (Chapter 5) indicated that the organisms collected were the source of the fecal pellets. Copepod nauplii dominated the total organism abundances (high concentrations of > 1200 no. l^{-1}), and there were more fecal pellets in the > 20 μm size fraction (Chapters 2 and 5). These fecal pellets, because of their size and density, are more likely to be retained within the water column and recycled (coprophagy, fragmentation, etc.), especially when food availability is low. Fahnenstiel et al. (1992) studied microzooplankton grazing and found that higher growth rates occurred in the plume compared to lower growth rates in the hypoxic region and that much of this growth is recycled within the surface layer by microzooplankton grazing. Higher microzooplankton grazing rates in summer and fall in the Mississippi River plume region indicated a more tightly coupled system during summer and fall compared to spring (Dagg & Ortner 1993). The strong similarities between the seasonal trends in fecal pellet carbon fluxes and meso- and microzooplankton communities and the high percentage of estimated primary production exported via fecal pellets, however, suggest that there is a strong coupling of zooplankton grazing with primary production in the spring.

CONCLUSIONS

Mesozooplankton distribution and community composition were studied in the vicinity of the moored sediment traps to identify the organisms which were the potential sources of fecal pellets collected. Samples were collected in 1991 (three month non-quantitative sampling) and in 1992 (six quantitative samples over a five month period).

The abundance and composition of the mesozooplankton community varied considerably between sample dates. Mesozooplankton were lowest in early to mid-July. This was possibly related to predation pressure or low food resources. The mesozooplankton samples did not show the same seasonal trends as the fecal pellet fluxes, but zooplankton abundances from the meso- and microzooplankton discrete sampling did. These differences were very likely the result of different sampling frequencies and methods.

Copepods were the dominant zooplankton, comprising 50 - 60% of the total, followed by oikopleurans, chaetognaths and meroplankton. Copepod numbers were strongly related to zooplankton abundance. There was a negative relationship between mesozooplankton abundance and surface water salinity. Copepod abundances were lower when the salinity was higher. This indicated an influence of the Mississippi River discharge on the distribution of copepod communities, which would likely result in high mesozooplankton abundances in spring following the high spring flow.

REFERENCES

BATHMANN, U. V., T. T. NOJI, M. VOSS, AND R. PEINERT. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar. Ecol. Prog. Ser. **38**: 45-51.

BOGDANOV, D. V., V. A SOKOLOV, AND N. S. KHROMOV. 1969. Regions of high biological and commercial productivity in the Gulf of Mexico and Caribbean sea. Oceanology **8**: 371-381.

DAGG, M. J., AND P. B. ORTNER. 1992. Mesozooplankton grazing and the fate of carbon in the northern Gulf of Mexico. p. 117-121. *In*: Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, AND _____. 1993. Grazing by meso- and micro-zooplankton in plume waters of the Mississippi and Atchafalaya Rivers. p. 27-29. *In* S. E. Lohrenz (ed.), Proceedings of the 1993 NECOP Data Workshop. University of Southern Mississippi, Gulf Coast Campus. Long Beach, Mississippi.

_____, AND W. E. WALSER JR. 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. Limnol. Oceanogr. **32**: 178-188.

_____, AND T. E. WHITLEDGE. 1991. Concentrations of copepod nauplii associated with the nutrient rich plume of the Mississippi River. Cont. Shelf Res. **11**: 1409-1423.

_____, P. ORTNER, AND F. AL-YAMANI. 1987. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. Fish. Bull. **86**: 319-330.

DINNEL, S. P., AND A. BRATKOVICH. 1993. Water discharge, nitrate concentration and nitrate flux in the lower Mississippi River. J. Mar. Sys. **4**: 315-326.

_____, AND W. J. WISEMAN, JR. 1986. Fresh water on the Louisiana and Texas Shelf. Cont. Shelf Res. **6**: 765-784.

DORTCH, Q., N. N. RABALAIS, R. E. TURNER, AND G. T. ROWE. 1994. Respiration rates and hypoxia on the Louisiana shelf. Estuaries **17**: 862-872.

FAHNENSTIEL, G. L., M. MARCOVITZ, M. J. MCCORMICK, D. G. REDALJE, S. L. LOHRENZ, H. J. CARRICK, AND M. J. DAGG. 1992. High growth and microzooplankton-grazing loss rates for phytoplankton populations from the Mississippi River plume region. p. 111-116. *In*: Proceedings, NECOP Synthesis Meeting, Publ. No. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

FLEMINGER, A. 1956. Taxonomic and distributional studies on the epiplanktonic calanoid copepods (Crustacea) of the Gulf of Mexico. Ph.D. Dissertation, Harvard University. 317 p.

GOVONI, J. J., AND A. J. CHESTER. 1990. Diet composition of larval *Leiostomus xanthurus* in and about the Mississippi River plume. J. Plank. Res. **12**: 819-830.

GOVONI, J. J., D. E. HOSS, AND D. R. COLBY. 1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnol. Oceanogr. **34**: 178-187.

HABERYAN, K. A. 1985. The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika. Limnol. Oceanogr. **30**: 1010-1023.

HOPKINS, T. L. 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. Deep-Sea Res. **29**: 1069-1083.

HOUDE, E. D., AND N. CHITTY. 1976. Seasonal abundance and distribution of zooplankton, fish eggs, and fish larvae in the eastern Gulf of Mexico, 1972 - 74. NOAA Tech. Rep. NMFS.SSRF-701: 1-18.

HOWEY, T. W. 1976. Zooplankton of the Gulf of Mexico: Distribution of displacement volume, occurrence of systematic groups, abundance and diversity among copepods. Ph.D. Dissertation. Louisiana State University, Baton Rouge, 195 p.

JUSTIC', D., N. N. RABALAIS, R. E. TURNER, AND W. J. WISEMAN JR. 1994. Stoichiometric nutrient balances and origin of coastal eutrophication. Mar. Pollut. Bull. : in press.

LAMPITT, R., T. T. NOJI, AND B. VON BODUNGEN. 1990. What happens to zooplankton faecal pellets? Implication for material flux. Mar. Biol. **104**: 15-23.

LOHRENZ, S. E., M. J. DAGG, AND T. E. WHITLEDGE. 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Cont. Shelf Res. **10**: 639-664.

LONGHURST, A. R. 1981. Significance of spatial variability, p. 415-441. *In* A. R. Longhurst [ed.], Analysis of Marine Ecosystems. Academic Press.

_____, AND W. G. HARRISON. 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. **35**: 881-889.

MADIN, L. P. 1982. Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar. Biol. **67**: 39-45.

MCCAVE, I. N. 1975. Vertical flux of particles in the ocean. Deep-Sea Res. **22**: 491-502.

NOJI, T. T. 1991. The influence of macrozooplankton on vertical particulate flux. Sarsia **76**: 1-9.

ORTNER, P. B., L. C. HILL, AND S. R. CUMMINGS. 1989. Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. Cont. Shelf Res. **9**: 387-402.

PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections J. Theoret. Biol. **13**: 131-144.

PIEPER, R. E., D. V. HOLLIDAY, AND G. S. KEPPEL. 1990. Quantitative zooplankton distributions from multifrequency acoustics. J. Plank. Res. **12**: 433-441.

PILSKALN, C. H., AND S. HONJO. 1987. The fecal pellet fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles **1**: 31-48.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. p. 35-47. *In* Tyson, R. V. and T. H. Pearson [eds.], Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58.

RILEY, G. A. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. J. Mar. Res. **1**: 60-83.

ROMAN, M. R., C. S. YENTSCH, A. L. GAUZENS, AND D. A. PHINNEY. 1986. Grazer control of fine-scale distribution of phytoplankton in warm-core Gulf Stream rings. J. Mar. Res. **44**: 795-813.

SHAW, R. F., J. H. COWAN, AND T. L. TILLMAN. 1985. Distribution and density of *Brevortia patronus* (Gulf menhaden) eggs and larvae in continental shelf waters of western Louisiana. Bull. Mar. Sci. **36**: 96-103.

SHANNON, C. E., AND W. WEAVER. 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois, p. 125.

SKLAR, F. H., AND R. E. TURNER. 1981. Plankton production in Louisiana coastal zone as influenced by the Mississippi River. Contrib. Mar. Sci. **24**: 93-106.

TURNER, J. T., AND J. G. FERRANTE. 1979. Zooplankton fecal pellets in aquatic ecosystems. BioScience **29**: 670-675.

TURNER, R. E., AND R. L. ALLEN. 1982. Plankton respiration rates in the bottom waters of the Mississippi River Delta Bight. Contr. Mar. Sci. **25**: 173-179.

_____, AND N. N. RABALAIS. 1991. Changes in Mississippi River water quality this century and implications for coastal food webs. BioScience **41**: 140-147.

_____, AND _____. 1994. Coastal eutrophication near the Mississippi River delta. Nature **368**: 619-621.

VILLATE, F. 1991. Annual cycle of zooplankton community in the Abre Harbour (Bay of Biscay): abundance, composition and size spectra. J. Plank. Res. **13**: 691-706.

WALSH, I., J. DYMAND, AND R. COLLIER. 1988. Rates of recycling of biogenic components of settling particles in the ocean derived from sediment trap experiments. Deep-Sea Res. **35**: 43-58.

WIEBE, P. 1970. Small-scale spatial distribution in oceanic zooplankton. Limnol. Oceanogr. **15**: 205-217.

CHAPTER 5

VERTICAL DISTRIBUTION OF FECAL PELLETS AND MESO- AND MICROZOOPLANKTON OF STRATIFIED WATERS ON THE LOUISIANA CONTINENTAL SHELF SUBJECT TO HYPOXIA

INTRODUCTION

The inner to mid-regions of the southeastern Louisiana continental shelf are subject to the freshwater effluents and nutrient fluxes of the combined flows of the Mississippi and Atchafalaya Rivers. Consequently, stratified, highly productive coastal waters dominate for much of the year (Rabalais et al. 1991, 1992, 1994a). Degradation of fluxed organic matter from surface waters to the lower water column and to the seabed contributes to the annual depletion of dissolved oxygen in the lower water column (Rabalais et al. 1991, Justic' et al. 1993, Kemp et al. 1992). Bottom water hypoxia (defined as < 2 mg O_2 l^{-1}) is extensive and often severe during mid-summer along most of the Louisiana coast (Fig. 1.1) (Rabalais et al. 1991). On the southeastern shelf off Terrebonne Bay, hypoxia develops as early as February - March, is persistent, extensive and severe from June - August, and sometimes may persist through September - October (Rabalais et al. 1991, 1992, 1994a).

The presence of oxygen-depleted bottom water may affect, either directly or indirectly, the abundance and distribution of zooplankton and, subsequently, the flux of organic matter from productive surface waters to the bottom. Copepods and copepod nauplii were in low abundance or absent from the oxygen depleted bottom waters (< 1 mg O_2 l^{-1}) of the Chesapeake Bay (Roman et al. 1993). Conversely, copepod abundances were highest in reaerated bottom waters during spring and summer (0900 - 1500 hours). Anoxia (no detectable oxygen) in the bottom waters disrupted normal diel migratory behavior of copepods which normally reside near the bottom during the day and migrate into the surface waters at night. Copepod abundances were highest at the

pycnocline throughout the day and the night when bottom waters were anoxic (Roman et al. 1993).

The importance of zooplankton in regulating primary production has been recognized. Mesozooplankton as well as microzooplankton graze a large proportion of the primary production stimulated by nutrients from the Mississippi River discharge (Dagg & Ortner 1992, 1993). The contribution of fecal pellets to the total amount of organic material flux to the sea floor varies from 1% to 90% (Pilskaln & Honjo 1987, Bathmann et al. 1987, Chapter 3), and is a function of seasonal surface productivity, zooplankton community structure and grazing activity of meso- and microzooplankton. The export of carbon from surface waters to the lower water column and sediments on the southeastern Louisiana shelf under the influence of the Mississippi River is high (approximately 67%) and exceeds the estimates of Suess (1980) for coastal waters (Chapter 3). Further, the fecal pellet carbon flux constitutes an average of 55% of the total particulate organic carbon flux from surface waters to the seabed (Chapter 3).

High temporal and spatial variability exists within the study area in the levels of primary production and distribution of phytoplankton biomass because of circulation patterns, winds, changes in freshwater and nutrient flux, and the variable interacting effects of nutrients, light and temperature on primary production. Variability at the base of the food web is likely to influence zooplankton distributions, and, conversely, variations in the zooplankton communities may affect the fate of primary production. Correspondence between chlorophyll *a* and high copepod naupliar concentrations was observed in the Mississippi River plume (Dagg et al. 1987). In addition, physical stratification of coastal and nearshore waters influenced by the Mississippi River provides a mechanism for the establishment of high concentrations of zooplankton (Dagg et al. 1987). Very little information is available on the temporal variability of zooplankton communities within the study area, and spatially broad studies are non-

existent. Even fewer studies address the distribution of zooplankton communities in relationship to hypoxia.

Indications of how the presence of low dissolved oxygen conditions in bottom waters might affect zooplankton distributions is seen in the work of Roman et al. (1993) from the Chesapeake Bay, where seasonal bottom water hypoxia is a dominant feature of the system. Copepod abundances were lowest in Chesapeake Bay in May - June when maximum chlorophyll biomass was available to support sufficient numbers of zooplankton (Roman et al. 1993). Possible mechanisms proposed for reduced zooplankton abundances were increased predation, reduced habitat (i.e., oxygen deficient bottom waters), inhibition of copepod egg hatching in oxygen depleted bottom waters and reduced copepod recruitment. Shifts in the abundance and distribution of zooplankton in a stratified water column where oxygen depletion is common and often severe in mid-summer could have two very different indirect effects on carbon flux. Lower copepod abundance (from reduced egg hatching and recruitment) could uncouple the grazing pressure from the primary production and more organic material might sink through the water, as cells or in aggregates. Shifts of zooplankton populations into the upper water column would likely lead to more remineralization and recycling of pelagic material by fragmentation and grazing of fecal pellets and, therefore, a reduction in the amount of material fluxed to the bottom. Concentrations of zooplankton just above the pycnocline might facilitate the biological pumping of fecal material into the lower water column. Any single or multiple combination of the potential effects could have positive or negative effects on organic material flux and, consequently, bottom water hypoxia.

I have examined the importance of fecal pellet flux in the transport of carbon to the lower water column where hypoxia is a dominant seasonal feature (Chapters 2 and 3). I now examine the distribution of meso- and microzooplankton communities and

the instantaneous occurrence of fecal pellets and how these differ temporally (both diel and seasonal) and spatially during the maximum extent of hypoxia.

OBJECTIVES

The objectives of this study were to:

1. determine the effect of water column stratification and oxygen deficiency in bottom waters on the distribution and abundance of meso- and microzooplankton and fecal pellets, at diel and monthly scales;
2. determine the effect of a range of bottom water oxygen values across a broad spatial scale in an area subject to hypoxia, ranging across a continuum from severe depletion to normoxic conditions;
3. determine the relationships between meso- and microzooplankton abundances and the instantaneous occurrence of fecal pellets;
4. examine the linkage between distributions of meso- and microzooplankton and the flux of fecal pellets at one location; and
5. examine how the distribution of meso- and microzooplankton and fecal pellets sampled in 'snapshots' might influence the fecal pellet flux into the sediment traps (Chapter 2).

METHODS

Sample Collections

Temporally intense collections were made monthly (March through September 1992) at station C6B off Terrebonne Bay within the core of hypoxic waters that forms annually on the southeastern Louisiana shelf (Fig. 1.1) (Rabalais et al. 1992, 1994a). Additionally, station C6B was sampled for 24 hours at approximately 6 hour intervals

during late July 1992 to examine diel variability. A broad spatial coverage of stations within a 2500 km^2 area, including station C6B, was targeted during late July and early August of 1991 and 1992, to examine zooplankton and fecal pellet distributions at stations from within and outside of the main hypoxic water mass (Table 5.1, Fig. 5.1). All times are reported as Central Daylight Savings Time, except the one on March 21, 1992, which is reported in Central Standard Time.

Water samples collected at station C6B were surface, 6.5 m, 14 m and bottom (19 m). Mid-water depths were selected to parallel the depth of the opening of the moored sediment traps at that station (Chapters 2 and 3). Surface and bottom water samples were collected at all other stations. Mid-water depths at stations other than C6B were targeted for above and below the pycnocline (or oxycline). Where a strong pycnocline (or oxycline) was not present, target depths were spaced evenly within the upper and lower water column, or above and below where the pycnocline was likely to occur.

Samples (10 to 15 l) were collected by bucket for surface or by Niskin bottles (triplicate 5 l on a CTD rosette sampler) or 30 l on an wire attached with a Hydrolab Surveyor 3 to determine depth. Water samples were transferred to spigotted carboys, and total volumes were recorded. The water sample was filtered through a nested series of 153 μm, 63 μm and 20 μm Nitex screens. The water in the carboy was continuously agitated to ensure a mixed sample. Zooplankton and fecal pellet samples collected on each screen were backwashed with filtered seawater (0.2 μm) into 60 ml bottles, preserved in 2.5% glutaraldehyde and refrigerated until further analysis.

Samples collected on the > 153 μm size fraction were analyzed under a dissecting microscope, and all organisms (meso- and microzooplankton) and fecal pellets were counted. The sample was split using a Folsom Plankton splitter if it was particularly dense, and the subsample was analyzed. The > 63 μm and the > 20 μm

Table 5.1. List of sample stations, dates, times collected, station depths, bottom water dissolved oxygen (DO mg l^{-1}) and for a continuum of dissolved oxygen concentrations

	Date	Time	Day/Night	Depth m	Bottom DO mg/l
Station					
RF2	8.3.92	16:55	D	16.3	0.05
C8	7.29.91	9:40	D	23.0	0.07
D2	7.28.91	21:10	N	12.5	0.07
C6B-4	7.27.91	16:20	D	19.0	0.14
C6B-5	7.31.91	0:01	N	19.0	0.54
C9	7.26.91	8:30	D	27.6	0.68
D2A	7.30.91	16:00	D	16.5	0.69
D6	7.30.91	0:35	N	71.7	1.80
C7	8.6.92	3:13	N	20.8	1.98
C6B-1	7.31.92	16:30	D	19.0	2.09
C11B	7.28.91	3:28	N	47.6	2.31
D'3	7.27.91	1:40	N	17.6	2.89
E2	8.2.92	11:09	D	8.3	3.53
Diel					
C6B	7.31.92	10:05	D	19.0	2.02
C6B-1	7.31.93	16:30	D	19.0	2.09
C6B-2	7.31.94	23:30	N	19.0	1.82
C6B-3	8.1.92	6:15	D	19.0	1.84
Monthly					
C6B	3.21.92	9:25*	D	19.0	0.86-1.39
C6B	4.10.92	16:15	D	19.0	1.14
C6B	5.26.92	11:02	D	19.0	2.36
C6B	6.17.92	17:25	D	19.0	0.07
C6B	7.31.92	16:30	D	19.0	2.09
C6B	8.12.92	11:03	D	19.0	0.12
C6B	9.18.92	11:36	D	19.0	4.56

* all times except this one time are Central Daylight Savings Time

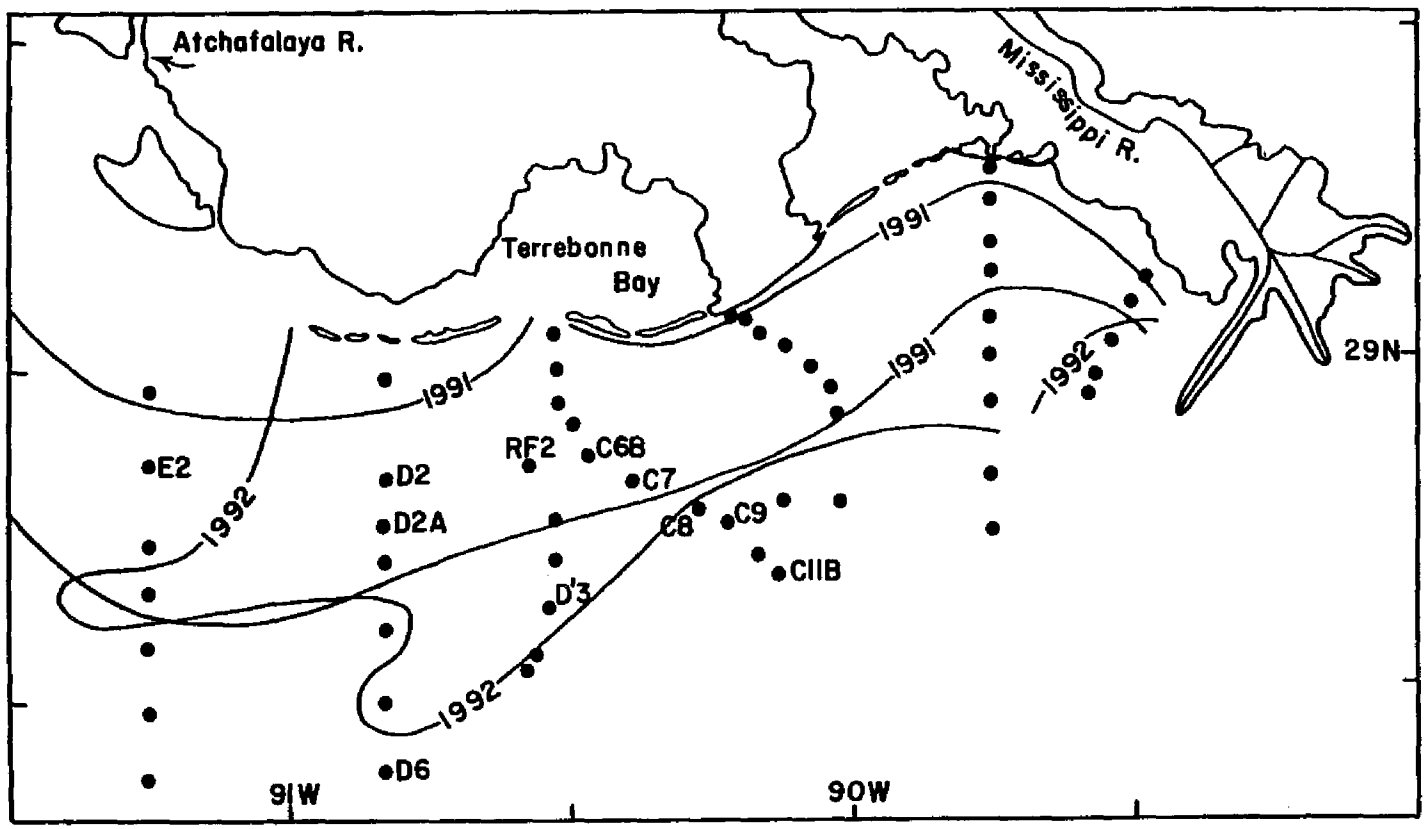


Figure 5.1. Location of stations sampled in late July and early August 1991 and 1992. Outlines of bottom water dissolved oxygen < 2 mg l^{-1} for survey periods 7/16-20/91 and 7/245-28/92 are shown; nearshore distribution of hypoxia extends to the coastline in 1992.

samples were stained with proflavin and filtered through an 8 μm cellulose filter which was mounted on a slide for enumeration on an epifluorescence microscope. Whole or part of the slide was analyzed, and Equations 2.1 and 2.2 in Chapter 2 were used to calculate the concentration of organisms and fecal pellets in the sample. The final concentrations (no. l^{-1}) of organisms and fecal pellets were calculated from the volume of water filtered.

Ancillary hydrographic data, including temperature, salinity, density and dissolved oxygen, were recorded with a Hydrolab Surveyor 3 or Sea Bird CTD unit during water column sampling. Biological data, which included water column pigment (chlorophyll *a* and phaeopigments) and nutrient concentrations, were collected at the same depths as the zooplankton sample and analyzed as described in Chapter 2.

Statistical Analyses

Data were categorized into total organism, copepod, copepod nauplius and fecal pellet concentrations (no. l^{-1}). Temporal variability was tested at two scales: (1) diel variability from station C6B (July 31 - August 1, 1992) and (2) monthly variability from station C6B (March through September 1992). Spatial variability was tested among stations collected with varying degrees of bottom water dissolved oxygen, ranging from 0.05 to 3.53 mg l^{-1} (Table 5.1, Fig. 5.1).

Each data set was tested for variability in the three main effects using a completely randomized design ANOVA with three factorial (4*4*3) treatment arrangements. The main effects and their interaction terms were fixed (tested by the random statement in the General Linear Model procedure of SAS (SAS Institute 1985)); therefore, each main effect and all the interaction terms were tested by the mean square error. The highest order interaction term was used as the error term, because there was no replication. The assumptions for normally distributed data and homogeneity of variance were tested for all dependent variables. Data were

transformed to $\log_{10}$ values to obtain normality and stabilize variance, when data were not normally distributed (Shapiro-Wilk statistics, $Pr > F = 0.0001$) and the mean values were proportional to their variances. The Type III sum of squares was used to compute mean square errors, because of the unbalanced data (Steel & Torrie 1980).

Tukey's studentized range test, a pair-wise comparison of means, was employed to specify variability within a treatment, when main effects were significant, because it is a more conservative test and has a family-wise error rate. However, the plots for each treatment were analyzed for variability when interaction terms were significant.

Relationships among the total number of organisms, copepods, copepod nauplii, and fecal pellets for each depth combination were determined by correlation analysis. The depth/date data were also correlated with environmental parameters of the water column, including temperature, salinity, dissolved oxygen, chlorophyll *a* and phaeopigment.

All statistical analyses were done using PC SAS version 6.04 (SAS Institute 1985).

RESULTS

Diel Variability

The vertical profiles of water column temperature, salinity and dissolved oxygen did not change substantially during the 24-h sampling at station C6B (Fig. 5.2). The water column was stratified, with a strong halocline, thermocline and oxycline at 10-11 m. The bottom water dissolved oxygen varied around 2 mg l^{-1}, the cut off for hypoxia, but it was not severely depleted.

The highest diversity occurred in the > 153 μm size fraction and was comprised of mesozoopankton, which were absent from the > 20 μm size fraction. Microzooplankton, represented by copepod nauplii, constituted the majority of

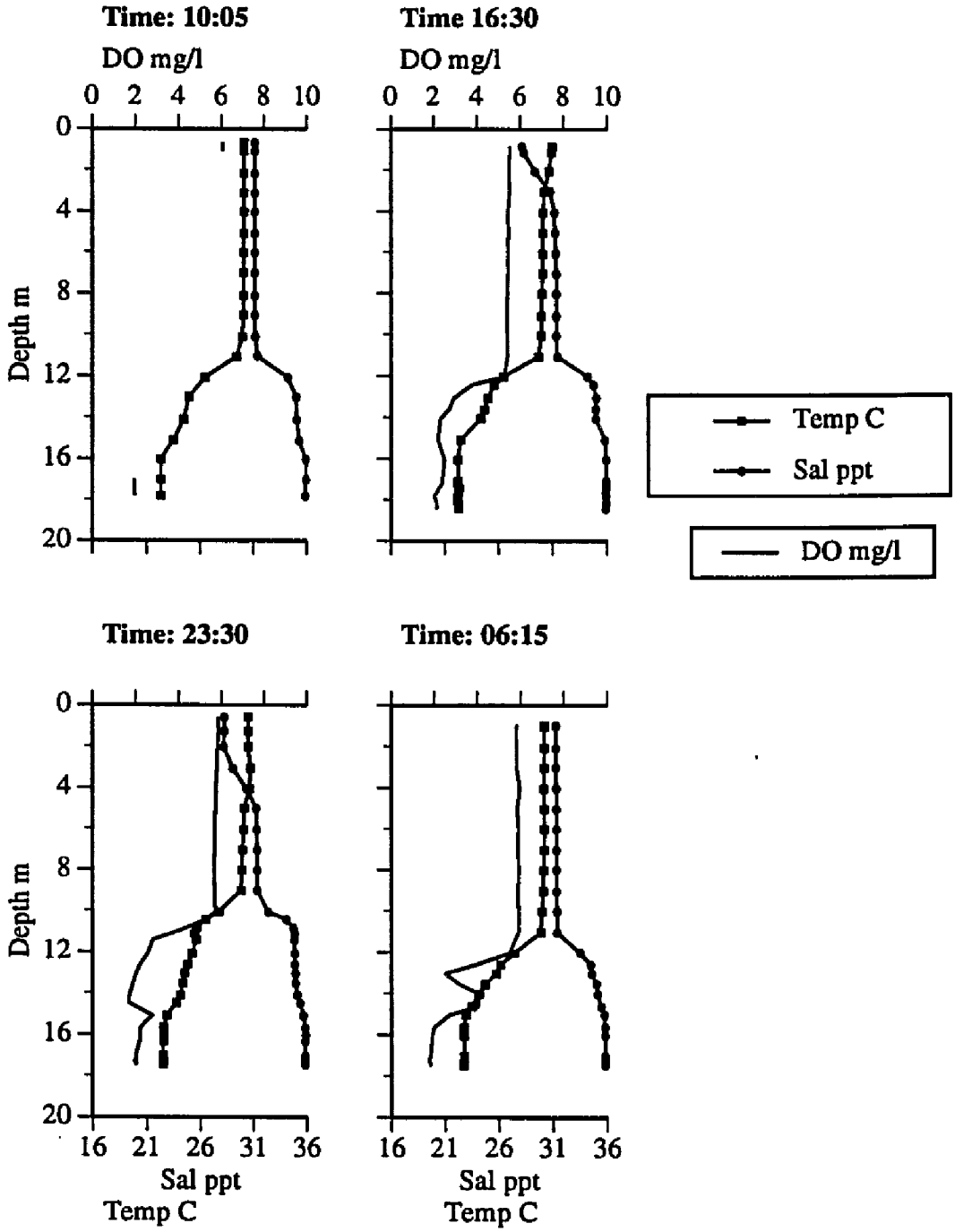


Figure 5.2. Vertical profiles of temperature (degree C), salinity (ppt), dissolved oxygen (DO mg l^{-1}) for 24 hour sampling at station C6B on July 31 - August 1, 1992.

organisms collected in the > 63 μm and the > 20 μm size fractions with occasional appearances in the > 153 μm size fraction. Most fecal pellets were collected in the > 20 μm size fraction.

Mesozooplankton in the > 153 μm size fraction were composed of copepods, copepod nauplii, oikopleurans, chaetognaths, meroplankton, and miscellaneous others. Copepods constituted an average of 32% of the total mesozooplankton in the > 153 μm size fraction, ranging from 10 to 50%. The relative proportions of taxonomic groups were similar in all depths with the exception of the surface, 6.5 m and 14 m samples at 10:05. Meroplankton dominated at 14 m at 10:05, constituting ~ 90% of the total organisms and comprising ~ 25% of the total at other times. Meroplankton included barnacle nauplius, zoea, protozoea, polychaete larva, balanoglossus tornaria, pilidium larva of nemertean, and ophiopluteus (echinoderm larva). Meroplankton constituted more than ~ 30% of the total zooplankton in the surface waters except at 10:05 (Fig. 5.3). There was a greater percentage of oikopleurans at 6.5 m at all times with the exception of 10:05, when copepods formed the dominant group (Fig. 5.3).

The average total organisms by depth was 119 l^{-1} (± 94 SD) ranging between 200 to 700 l^{-1} with the lowest and highest values both at 14 m (26 to 398 l^{-1}). The densities of total organisms were significantly different between times, depths and size fractions (Tables 5.2 and 5.3). The highest concentration of total organisms occurred at 16:30, at 14 m and in the > 63 μm size fraction (Table 5.3, Fig. 5.4). The time*depth interaction term was also significant. The total organisms were lowest at 10:05, in all depths and size fractions. The mean concentration of total organisms was highest in the > 63 μm size fraction and lowest in the > 153 μm size fraction (Fig. 5.4). The densities of total organisms were higher in the lower water column than in the upper, because of a high number of total organisms at 14 m in the > 63 μm and the > 20 μm size fractions (Fig. 5.4). Numbers of total organisms in the upper water column were elevated at 23:30 at 6.5 m and at the surface because of higher densities in the > 20 μm size

Table 5.2. Three factorial completely randomized design ANOVA (P > F) for concentration (no. /liter) of total organisms, copepods, copepod nauplii and fecal pellets for diel samples at station C6B (July 31 - August 1, 1992).

	df	Total Organisms P > F	Copepods P > F	Copepod Nauplii P > F	Fecal Pellets** P > F
Pr < W		0.8311	0.7363	0.3594	0.7337
Model	29	0.0188*	0.0345*	0.1281	0.0382*
Time	3	0.0143*	0.0165*	0.1488	0.2471
Depth	3	0.0135*	0.0200*	0.4751	0.0340*
Size Fraction (SF)	2	0.0085*	0.3619	0.0077*	0.0001*
Time*Depth	9	0.0210*	0.0722	0.1175	0.8452
Time*SF	6	0.6311	0.1711	0.8951	0.8571
Depth*SF	6	0.8201	0.6257	0.7707	0.3801

* significant at alpha = 0.05

** log10 transformed data

Table 5.3. Tukey's studentized range test for concentration (no./liter) of total organisms, copepods, copepod nauplii, and fecal pellets collected from station C6B during 24 hours (July 31 - August 1, 1992). Means with the same letter are not significantly different (alpha = 0.05).

	Number	Total Organisms no./ liter	Copepods * no./ liter	Copepod Nauplii* no./ liter	Fecal Pellets* no./ liter
Time					
10:05	10	17.36 B	3.395 B	12.13 A	7.04 A
16:30	12	58.66 A	21.605 A	35.99 A	38.8 A
23:30	12	46.97 AB	8.929 AB	34.55 A	12.6 A
6:15	12	35.54 AB	4.419 B	27.82 A	19.7 A
Depth					
Surface	12	22.15 B	2.487 B	18.16 A	14 AB
6.5 m	11	27.66 AB	3.204 B	20.58 A	2.83 B
14 m	11	59.85 A	21.733 A	40.04 A	55.1 A
Bottom	12	48.87 AB	13.103 AB	32.97 A	9.82 AB
Size Fraction					
>153 µm	15	20.29 B	7.743 A	2.61 B	1.63 B
>63 µm	15	55.14 A	12.579 A	35.03 A	3.83 B
>20 µm	16	43.46 AB	na	42.04 A	52.6 A

* analysis was performed on log10 transformed data but means are presented as untransformed data

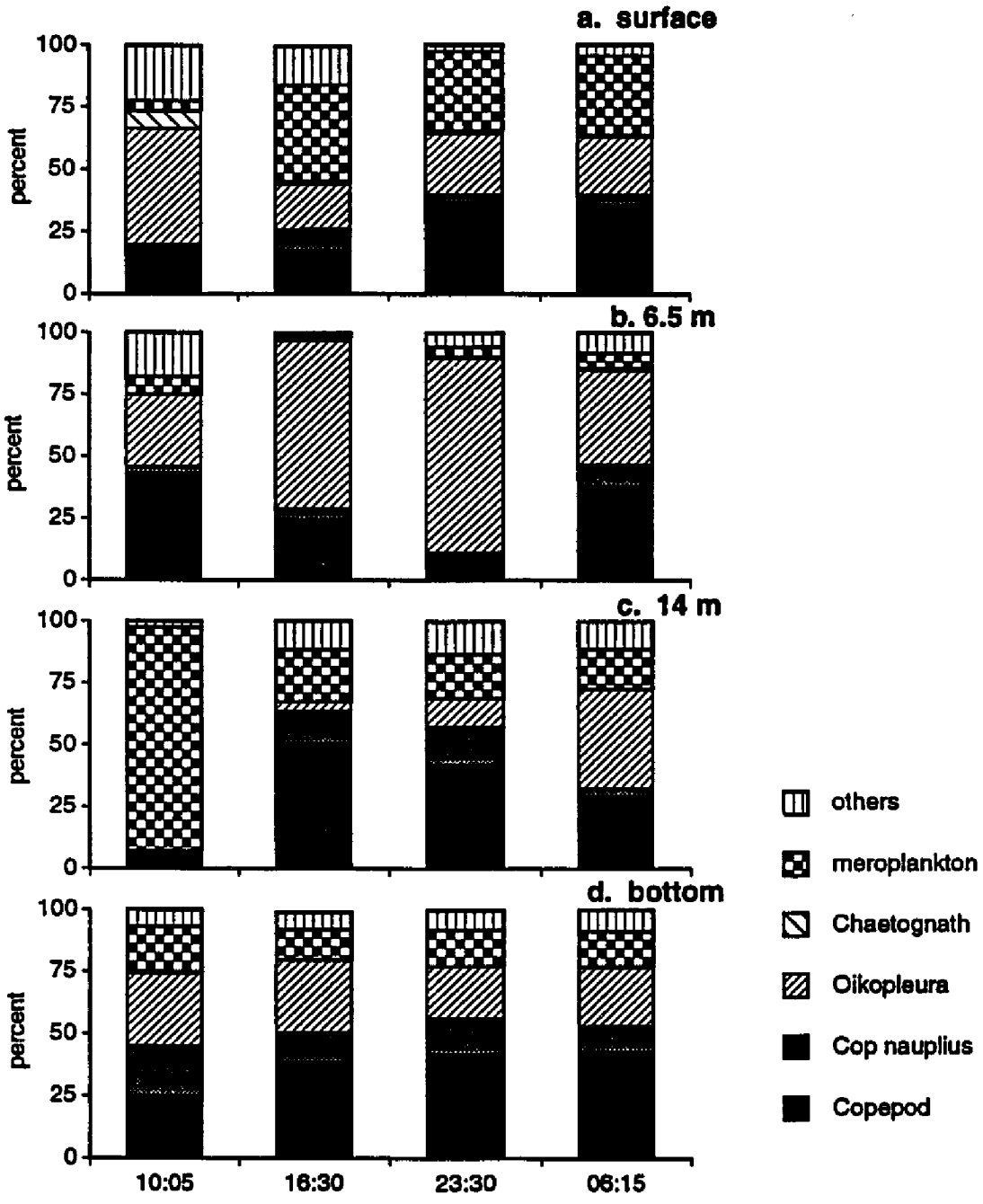


Figure 5.3. Percent composition of mesozooplankton in > 153 μm size fraction at discrete depths during 24-h sampling at station C6B sampling (July 31 - August 1, 1992). Times are Central Daylight Savings Time.

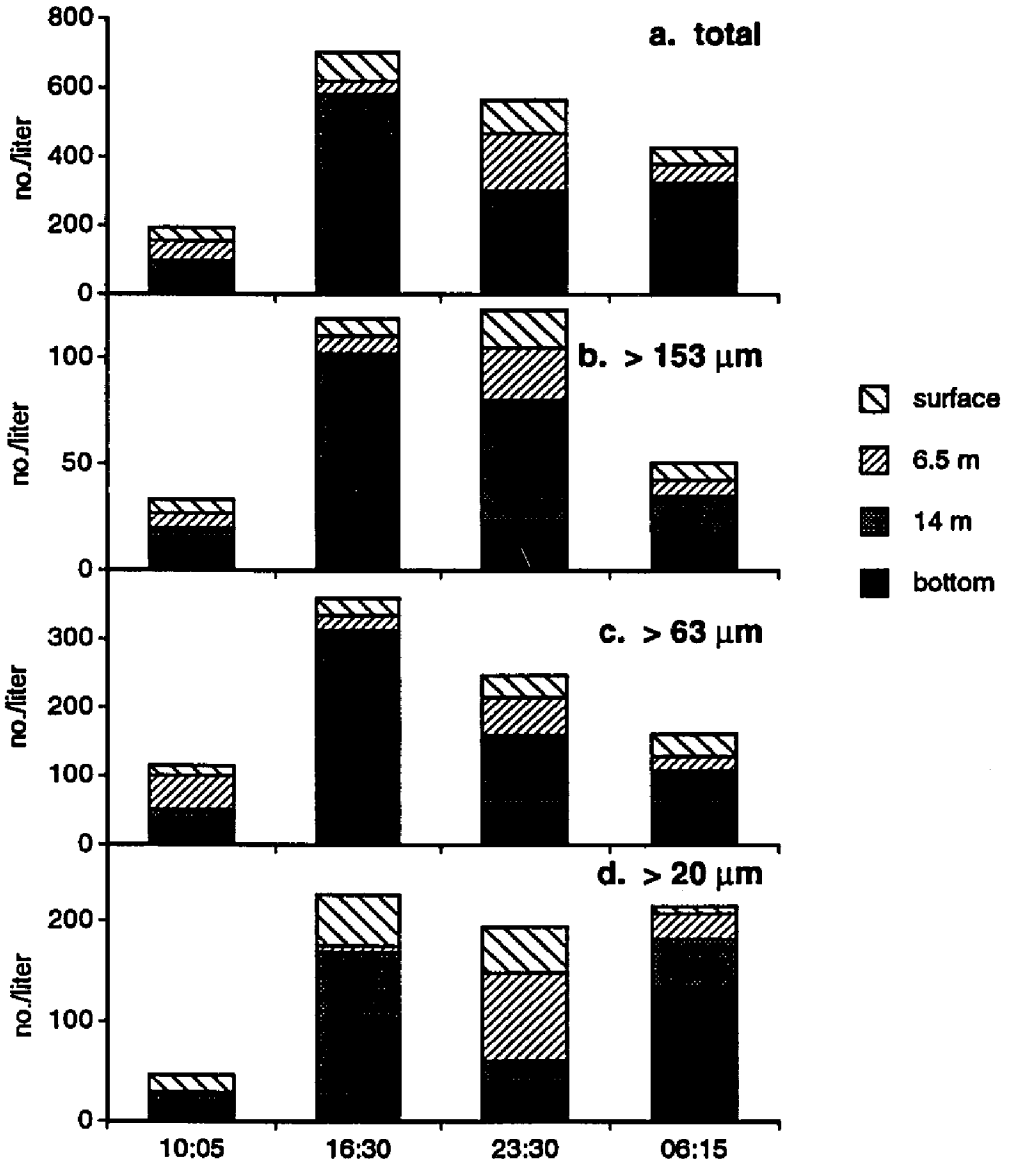


Figure 5.4. Change in concentration of total organisms (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B during 24-h sampling (July 31 - August 1, 1992). Times are Central Daylight Savings Time.

fraction (mostly copepod nauplii). A very high r^2 (0.98) existed between total organisms and copepod nauplii concentrations.

The average copepod density by depth was low 19 l^{-1} (± 28 SD) during the 24-h sampling, being highest at 14 m depth and ranging from 1 to 100 l^{-1}. The copepod concentrations varied with time and with depth (Table 5.2). Highest concentrations of copepods occurred in the lower water column (at 14 m and the bottom) at 16:30 in both the > 153 μm and > 63 μm size fractions (Table 5.3, Fig. 5.5).Copepods were not found in the > 20 μm size fraction, as expected given the sampling technique. Copepod abundance was lowest at 10:05 in both size fractions and mostly distributed in the upper water column (surface and 6.5 m) (Fig. 5.5). There was a shift of copepods to the upper water column at 23:30 and 06:15 compared to 16:30 when copepods were concentrated in the lower water column.

The average copepod nauplii density by depth was 79 l^{-1} (± 63 SD) ranging from 11 to 251 l^{-1}. There were no significant differences in the concentrations of copepod nauplii with time or depth, probably due to the high variances. The densities of copepod nauplii were significantly higher in the > 63 μm and > 20 μm size fractions than in the > 153 μm size fraction, as expected given the sampling technique (Table 5.3). The concentration of copepod nauplii was higher in the lower water column (14 m and bottom) in all size fractions at 16:30 and 06:15 compared to at 23:30 and 10:05 when more copepod nauplii were in the upper water column (surface and 6.5 m) (Fig. 5.6).

The average fecal pellet concentration by depth was 58 l^{-1} (± 98 SD) ranging from 1 to 398 fecal pellets l^{-1}. The concentrations of fecal pellets were significantly different between depths and between size fractions (Table 5.2). Fecal pellet numbers were highest at 14 m depth in the > 20 μm size fraction (Table 5.3, Fig. 5.7). There were more smaller fecal pellets, which dominated the > 20 μm size fraction, than the larger fecal pellets in other size fractions (Table 5.3). The highest numbers of fecal

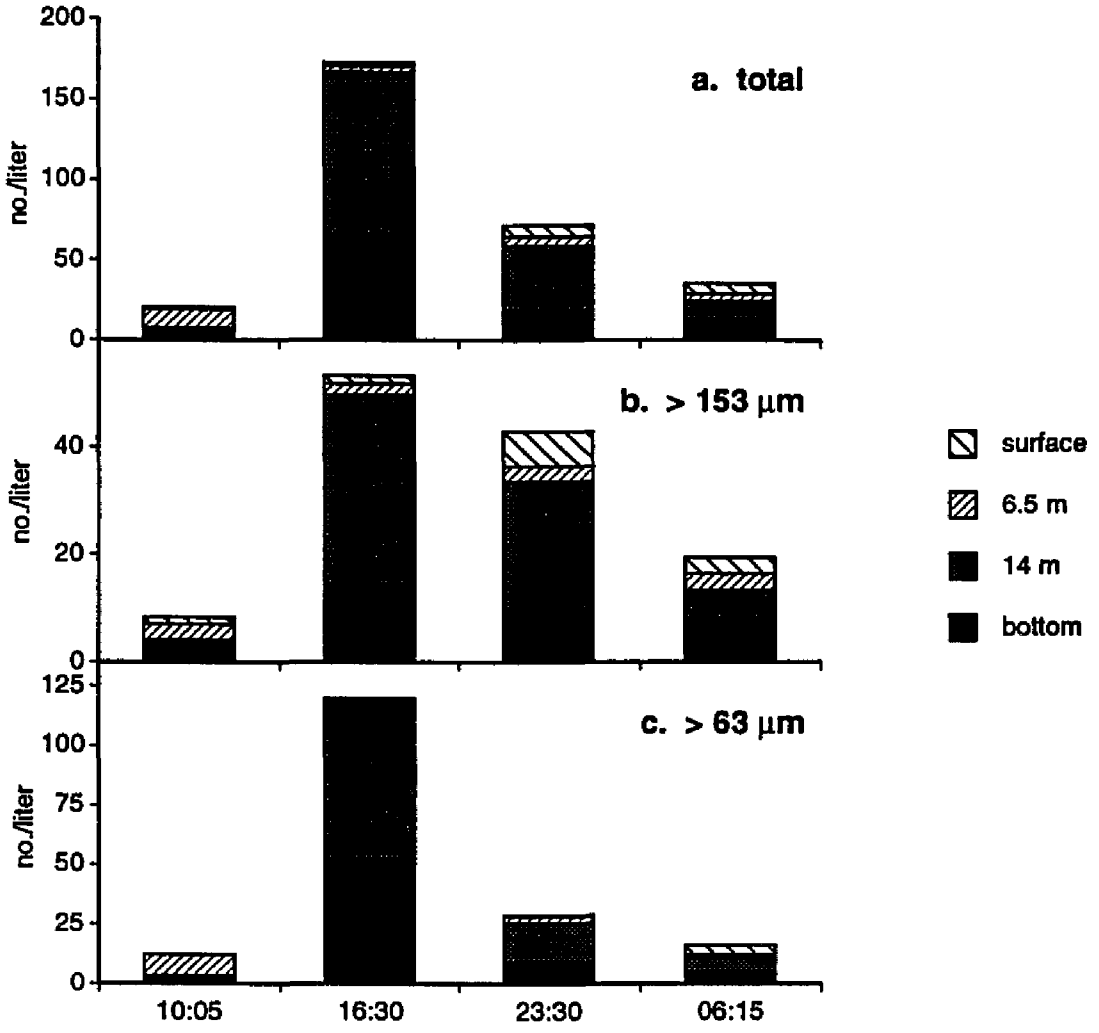


Figure 5.5. Change in concentration of copepods (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B during 24-h sampling (July 31 - August 1, 1992). Times are Central Daylight Savings Time.

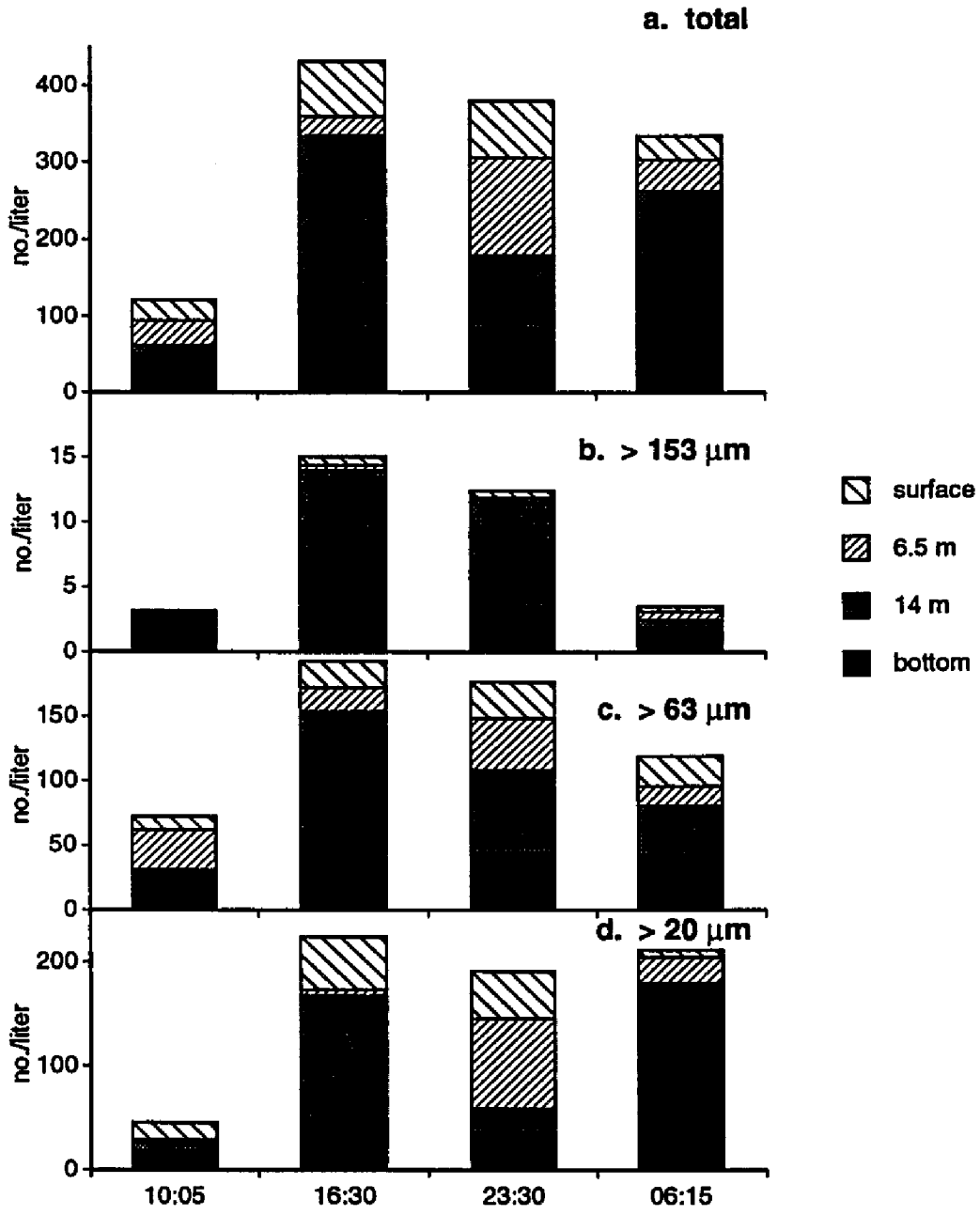


Figure 5.6. Change in concentration of copepod nauplii (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B during 24-h sampling (July 31 - August 1, 1992). Times are Central Daylight Savings Time.

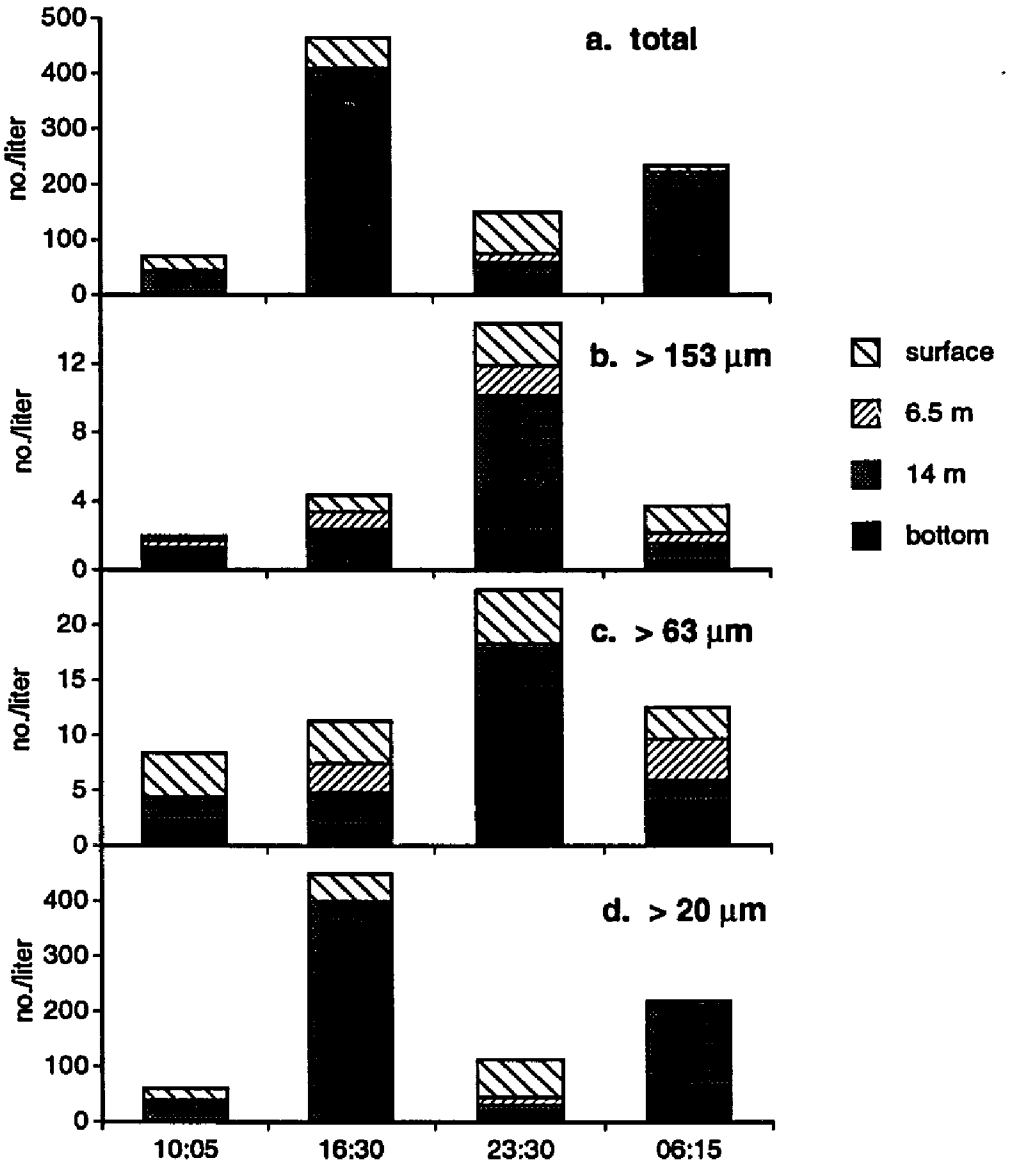


Figure 5.7. Change in concentration of fecal pellets (no. l^{-1}) at four depths for size fractions indicated and total of all sizze fractions at station C6B during 24-h sampling (July 31 - August 1, 1992). Times are Central Daylight Savings Time.

pellets occurred at 16:30, and were mostly at 14 m depth (Fig. 5.7); this paralleled high concentrations of copepods and copepod nauplii in the lower water column at the same time (Fig. 5.6). The low number of fecal pellets at 10:05 was related to lower number of organisms. The higher number of fecal pellets in the surface waters at 23:30 in all size fractions and at 06:15 in the lower water column (14 m and the bottom) were also related to higher numbers of copepods and copepod nauplii in the upper water column at 23:30 and their movement back to depth at 06:15.

Total organisms were positively correlated with the number of copepods and copepod nauplii (Table 5.4). Fecal pellet concentrations were positively correlated with the number of total organisms, copepods and copepod nauplii. Relationships between organisms and hydrographic data were not significant, because there was not much difference in the water column structure during the 24-h sampling (Fig. 5.2).

Monthly Variability

The water column at station C6B from March through September was usually stratified, and the density structure was controlled primarily by the salinity (Figs. 5.8 and 2.2). The pycnocline was usually located between 8 and 15 m. Continuous bottom oxygen data for C6B indicated fluctuations above and below 2 mg l^{-1} from March through August (Fig. 2.4). Sampling on March 21, while conducted during a period of hypoxia, followed several days of aerated bottom waters (Figs. 5.8 and 2.4). Bottom water dissolved oxygen was low during and several days prior to the sampling in April. The May sample was collected when the bottom waters were near 2 mg l^{-1}, but followed a severely hypoxic period. The June sample was in the middle of an extended period of severely hypoxic, anoxic bottom waters. Bottom water during the July sample fluctuated around 2 mg l^{-1} The reoxygenation resulted from the intrusion of colder, saltier water from offshore (N. N. Rabalais pers. comm.), but was followed by another severely hypoxic period during which the August sample was taken. Hurricane

Table 5.4. Pearson correlation coefficients matrix showing relationship between concentration (no./liter) of total organisms, copepods, copepod nauplii and fecal pellets with zooplankton constituents, fecal pellets and ancillary hydrographic data from station C6B during 24 hours (July 31 - August 1, 1992); (n = 28).

	Total Organisms	Copepods	Copepod Nauplii	Fecal Pellets
Total Organisms	1.00			
Copepods	0.86 *	1.00		
Copepod Nauplii	0.96 *	0.70 *	1.00	
Fecal Pellets	0.78 *	0.69 *	0.77	1.00
Dissolved oxygen (mg/l)	-0.47 *	-0.49 *	-0.39	-0.21
Salinity (ppt)	0.41	0.45	0.33	0.20
Temperature (degrees C)	-0.45 *	-0.48 *	-0.38	-0.24
Chlorophyll a (μg/l)	-0.24	-0.12	-0.32	-0.12
Phaeopigment (μg/l)	0.11	0.22	0.01	0.16

* significant at alpha = 0.05

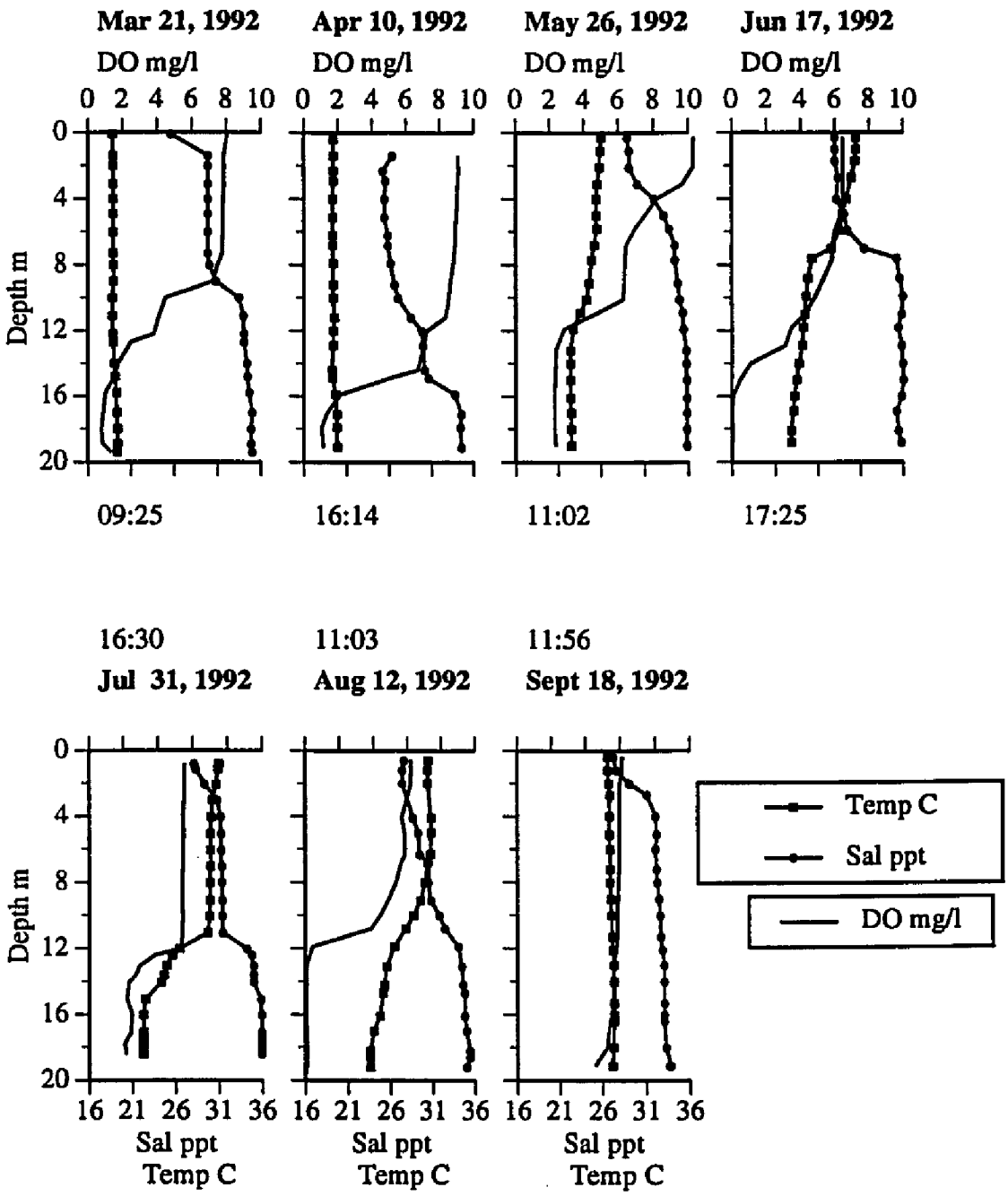


Figure 5.8. Vertical profiles of temperature (degree C), salinity (ppt) and dissolved oxygen (DO mg l^{-1}) at station C6B from March through September 1992. Times are Central Daylight Savings Time (except March which is Central Standard Time).

Andrew moved through the study area on August 25 and mixed the water column, a condition which persisted through September, because of the passage of several cold fronts.

Mesozooplankton in > the 153 μm size fraction were composed of a high percentage of copepods and copepod nauplii at all depths, but the percent composition varied with month and depth (Fig. 5.9). Copepods comprised an average of 55% of the total concentration ranging from 15 and 85%. Meroplankton (included mostly benthic larvae) comprised nearly 80% of the total community in the bottom waters in June when the lower 3 m of the water column were severely hypoxic, but decreased to ~ 20% in July when the mesozooplankton community was more diverse. Meroplankton comprised ~ 90% of the total community at 14 m in August, when bottom waters were also severely hypoxic (lower 7 m).

The average density of total organisms by depth was 189 l^{-1} (± 147 SD), ranging from 12 to 575 l^{-1}. The concentration of total organisms was significantly different between months and between size fractions with a significant month*size fraction interaction, but did not differ by depth (Table 5.5). The total concentration of organisms were highest in March and April and lowest in June (Table 5.6). The high concentration of total organisms in the > 63 μm and the > 20 μm size fractions was due to a high abundance of copepod nauplii (Figs. 5.10 and 5.12). The total organisms were evenly distributed at all depths across all months (Table 5.6). There were more total organisms in the upper water column (surface and 6.5 m) in June, August and September, and more in the lower water column (14 m and bottom) in March, April, May and July (Fig. 5.10).

The average density of copepods by depth was 33 l^{-1} (± 47 SD), ranging between 1 and 245 l^{-1}. Copepod concentrations varied between months and with depths, but there were no significant differences in copepod concentrations between size fractions (copepods were not found in the > 20 μm size fraction) (Tables 5.5 and

Table 5.5. Three factorial completely randomized design ANOVA (P > F) for concentration (no./liter) of total organisms, copepods, copepod nauplii and fecal pellets collected from station C6B from March - September 1992.

	df	Total Organisms P > F	Copepods** P > F	Copepod Nauplii** P > F	Fecal Pellets** P > F
Pr < W		0.6602	0.7329	0.8823	0.9162
Model	47	0.0011*	0.0007*	0.0001*	0.0002*
Months	6	0.0018*	0.0003*	0.0001*	0.0418*
Depth	3	0.1825	0.0113*	0.3453	0.5746
Size Fraction (SF)	2	0.0001*	0.3564	0.0001*	0.0001*
Month*Depth	18	0.1425	0.0012*	0.0479*	0.2854
Month*SF	12	0.0088*	0.6731	0.8756	0.4192
Depth*SF	6	0.4241	0.0602	0.6265	0.3588

* significant at alpha = 0.05

** log10 transformed data

Table 5.6. Tukey's studentized range test for concentration (no./liter) for total organisms, copepods, copepod nauplii, and fecal pellets collected from station C6B during March - September 1992. Means with the same letter are not significantly different (alpha = 0.05).

	Number	Total Organisms no./ liter	Copepods * no./ liter	Copepod Nauplii* no./ liter	Fecal Pellets* no./ liter
Month					
March	12	125.92 A	25.09 A	99.93 AB	125.7 AB
April	10	99.90 AB	8.01 BDC	100.22 A	114.1 A
May	12	56.58 ABC	40.75 AB	23.26 BC	85.57 AB
June	12	24.26 C	6.89 D	20.34 C	80.11 AB
July	10	58.66 ABC	14.40 BCD	35.99 ABC	38.79 B
August	12	51.79 BC	12.19 CD	43.74 B	34.75 AB
September	11	44.61 BC	17.40 ABC	30.17 ABC	122.8 AB
Depth					
Surface	21	64.91 A	8.25 B	55.29 A	33.89 A
6.5 m	19	61.44 A	9.69 B	48.35 A	88.41 A
14 m	20	88.38 A	20.04 A	71.77 A	71.96 A
Bottom	19	51.44 A	34.07 A	32.96 A	151.5 A
Size Fraction					
>153 µm	24	20.27 B	12.30 A	3.15 B	3.03 C
>63 µm	27	77.62 A	25.78 A	50.33 A	55.76 B
>20 µm	28	104.56 A	4.00 A	101.32 A	186.9 A

* analysis was performed on log10 transformed data but means are presented as untransformed data

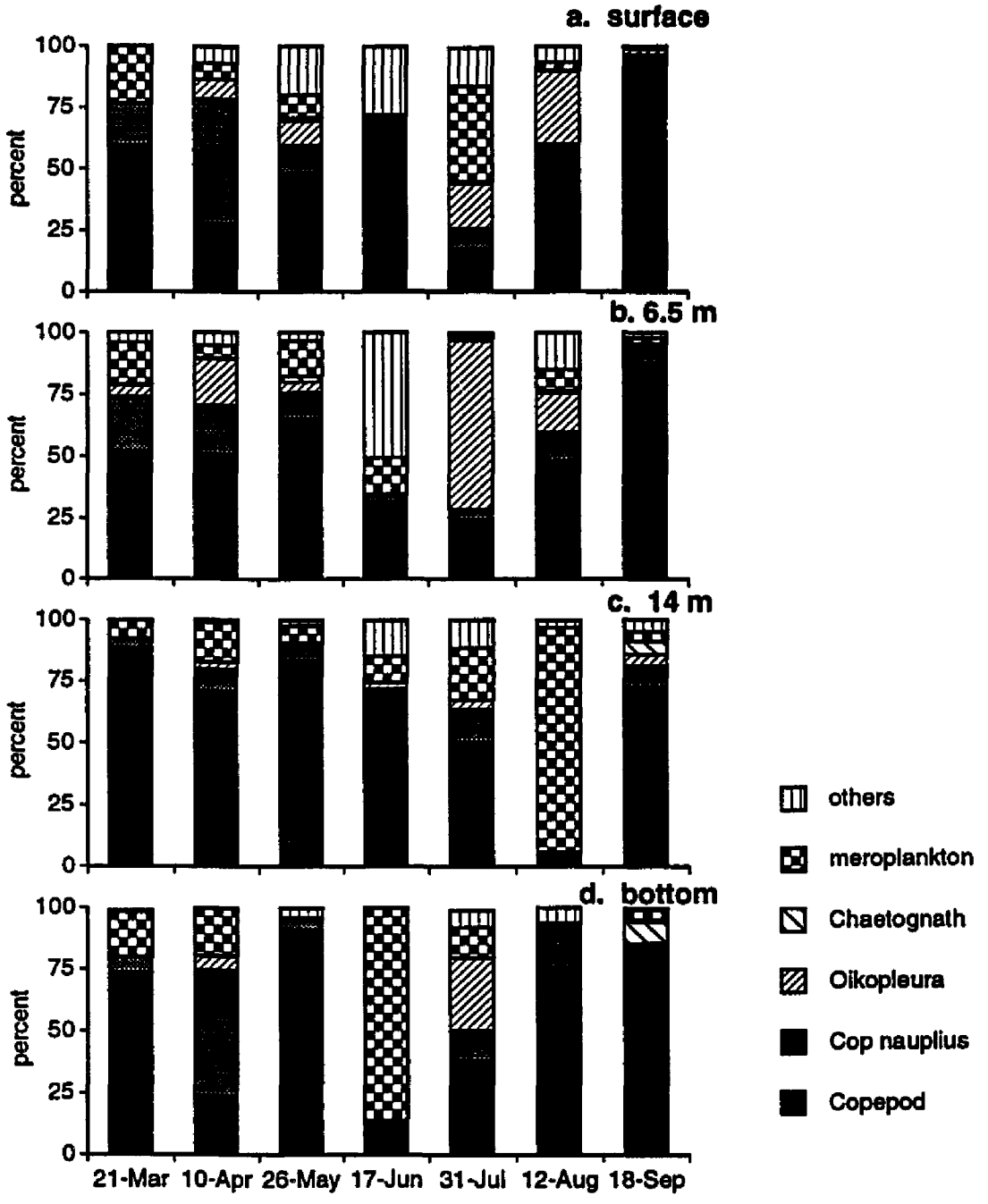


Figure 5.9. Percent composition of mesozooplankton in >153 μm size fraction at discrete depths at station C6B from March - September 1992.

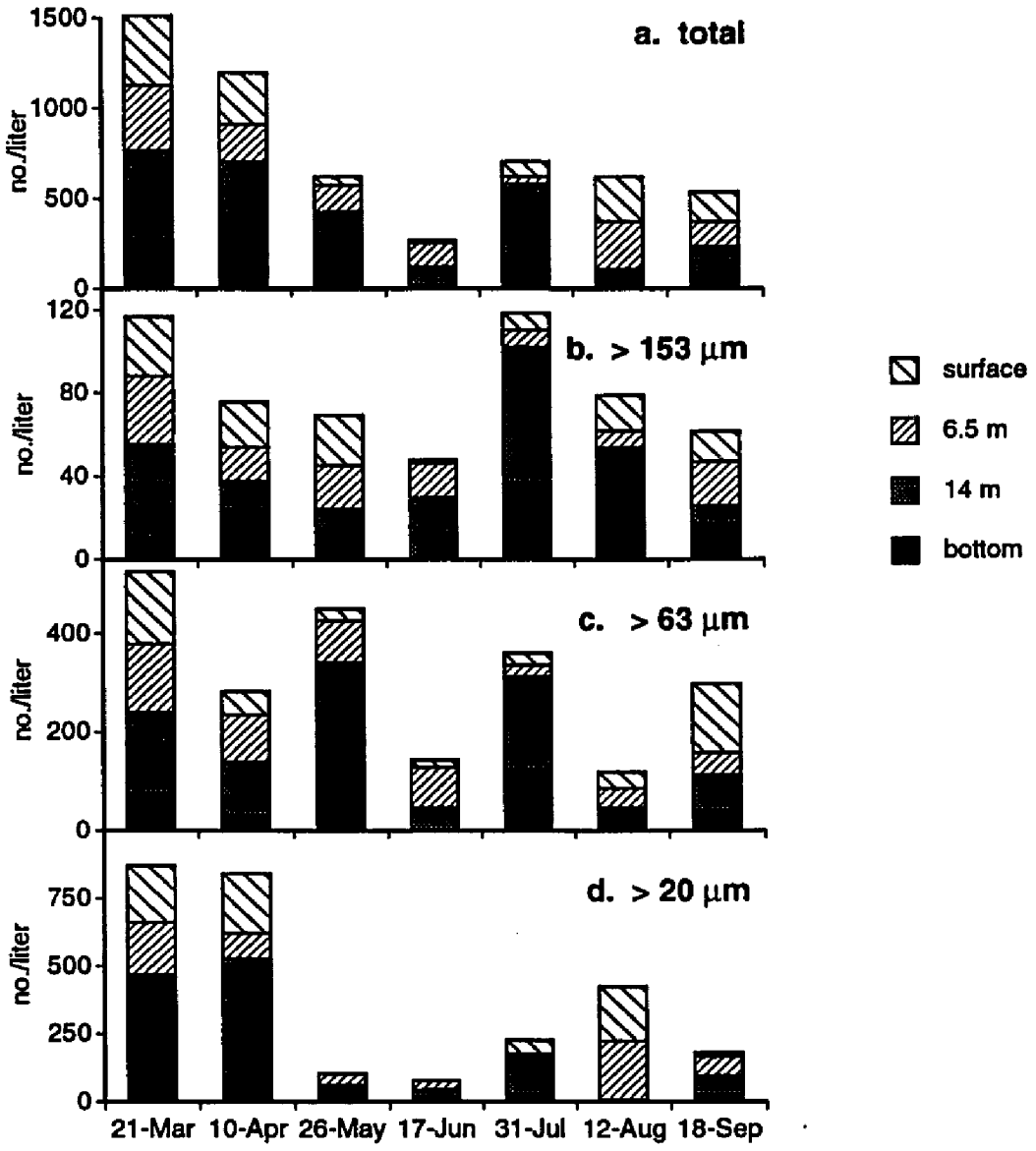


Figure 5.10. Change in concentration of total organisms (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B from March through September 1992.

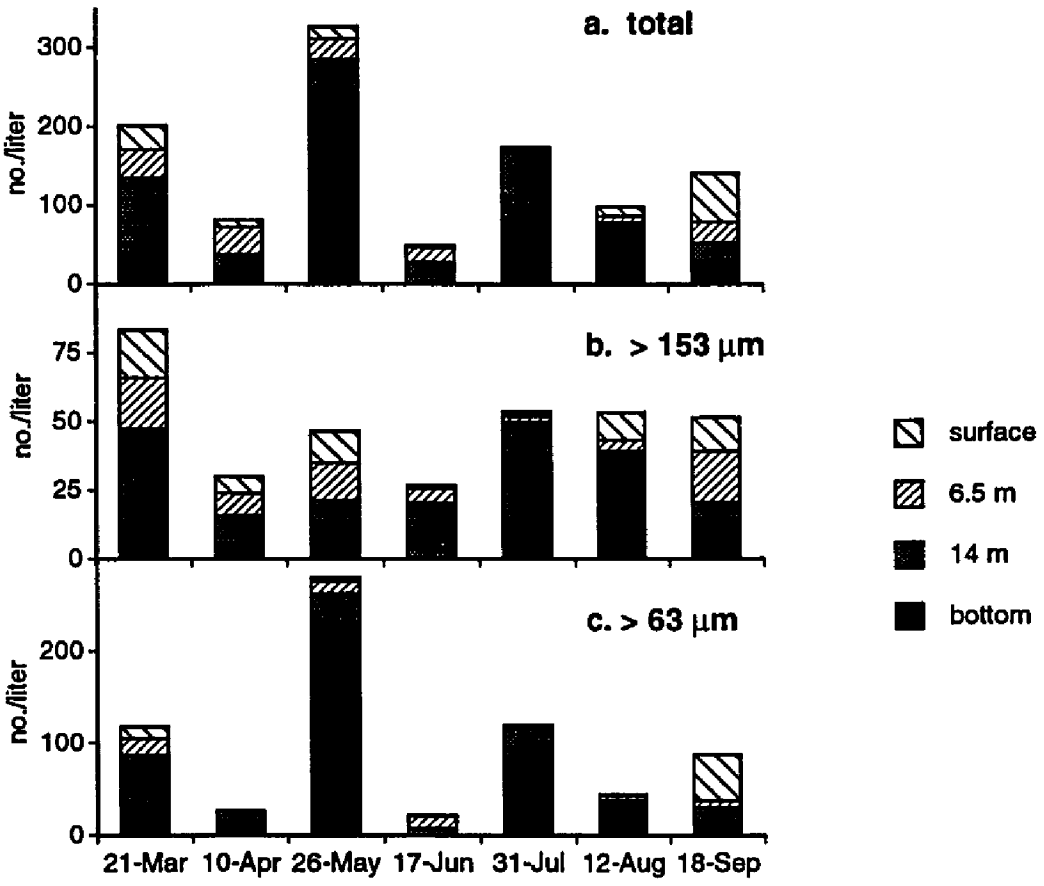


Figure 5.11. Change in concentration of copepods (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B from March through September 1992.

5.6). Highest mean concentrations of copepods occurred in March and May, were lowest in April and June, and were intermediate in July, August and September (Table 5.6, Fig. 5.11). More copepods were found in the lower water column (14 m and bottom) except in June when bottom waters were severely hypoxic (0.1 mg l^{-1}). The extremely low oxygen concentrations in the lower water column in August, however, did not exclude copepods (Figs. 5.8 and 5.11).

The average density of copepod nauplii by depth was 135 l^{-1} (± 134 SD) ranging from 5 to 548 l^{-1}. The densities of copepod nauplii were significantly different between months and between size fractions, but not depth (Tables 5.5 and 5.6). Concentrations of copepod nauplii were significantly highest in March and in April, decreased from May to June and increased again in July through September (Fig. 5.12). The concentrations of copepod nauplii were significantly higher in both the > 63 µm and the > 20 µm size fractions (Table 5.6, Fig. 5.12).

The average fecal pellet concentration by depth was 231 l^{-1} (± 340 SD), ranging between 1 and 1225 l^{-1}. Fecal pellet concentrations were significantly different between months and between size fractions, but not by depth (Table 5.5). Concentrations of fecal pellets were highest early in the year (March through April), declined in May through June, were lowest in July and August, then increased substantially in September (Table 5.6, Fig. 5.13). More fecal pellets were present in the > 20 µm size fraction. More fecal pellets were usually present in the lower water column (14 m and bottom) except in June and September when more were present in the upper water column (surface and 6.5 m) (Fig. 5.13).

Copepod nauplii comprised most of the total organisms at all depths except the bottom where copepods were more abundant (Table 5.7). The number of copepods was not related with the number of organisms or copepod nauplii as it was in the 24-h sampling. Fecal pellet concentration was positively correlated with copepod nauplii at the bottom. The concentrations of total organisms and copepod nauplii were negatively

Table 5.7. Pearson correlation coefficients matrix showing relationship between concentration (no. l^{-1}) of total organisms, copepods, copepod nauplii and fecal pellets with zooplankton constituents, fecal pellets and ancillary hydrographic data from station C6B during March - September 1992.

	Total Organisms	Copepods	Copepod Nauplii	Fecal Pellets
Surface: n = 7				
Total Organisms	1.00			
Copepods	0.28	1.00		
Copepod Nauplii	0.99 *	0.13	1.00	
Fecal Pellets	-0.49	-0.41	-0.44	1.00
Dissolved oxygen (mg/l)	0.46	0.05	0.44	-0.30
Salinity (ppt)	-0.90 *	-0.30	-0.89 *	0.18
Temperature (degrees C)	-0.73	-0.26	-0.72	0.36
Chlorophyll a (µg/l)	0.07	-0.14	0.11	-0.28
Phaeopigment (µg/l)	0.46	-0.08	0.54	-0.16
6.5 m: n = 7				
Total Organisms	1.00			
Copepods	0.54	1.00		
Copepod Nauplii	0.99 *	0.54	1.00	
Fecal Pellets	-0.23	0.18	-0.21	1.00
Dissolved oxygen (mg/l)	0.51	0.81 *	0.51	-0.22
Salinity (ppt)	-0.36	-0.30	-0.36	0.22
Temperature (degrees C)	-0.59	-0.92 *	-0.59	0.12
Chlorophyll a (µg/l)	0.31	0.64	0.30	-0.26
Phaeopigment (µg/l)	0.01	0.45	0.02	-0.28
14 m: n = 7				
Total Organisms	1.00			
Copepods	0.53	1.00		
Copepod Nauplii	0.97 *	0.33	1.00	
Fecal Pellets	-0.12	0.41	-0.23	1.00
Dissolved oxygen (mg/l)	0.74 *	0.18	0.79 *	-0.26
Salinity (ppt)	-0.60	0.29	-0.74 *	0.50
Temperature (degrees C)	-0.73 *	-0.30	-0.74 *	-0.20
Chlorophyll a (µg/l)	0.97 *	0.37	0.98 *	-0.21
Phaeopigment (µg/l)	-0.46	-0.48	-0.39	-0.11
Bottom: n = 7				
Total Organisms	1.00			
Copepods	0.71	1.00		
Copepod Nauplii	0.42	-0.23	1.00	
Fecal Pellets	0.41	-0.17	0.90 *	1.00
Dissolved oxygen (mg/l)	0.52	0.02	0.41	0.40
Salinity (ppt)	0.30	0.43	-0.22	-0.21
Temperature (degrees C)	-0.46	0.01	-0.78	-0.79 *
Chlorophyll a (µg/l)	0.23	-0.05	0.18	-0.16
Phaeopigment (µg/l)	-0.15	-0.10	-0.23	-0.05

* significant at alpha = 0.05

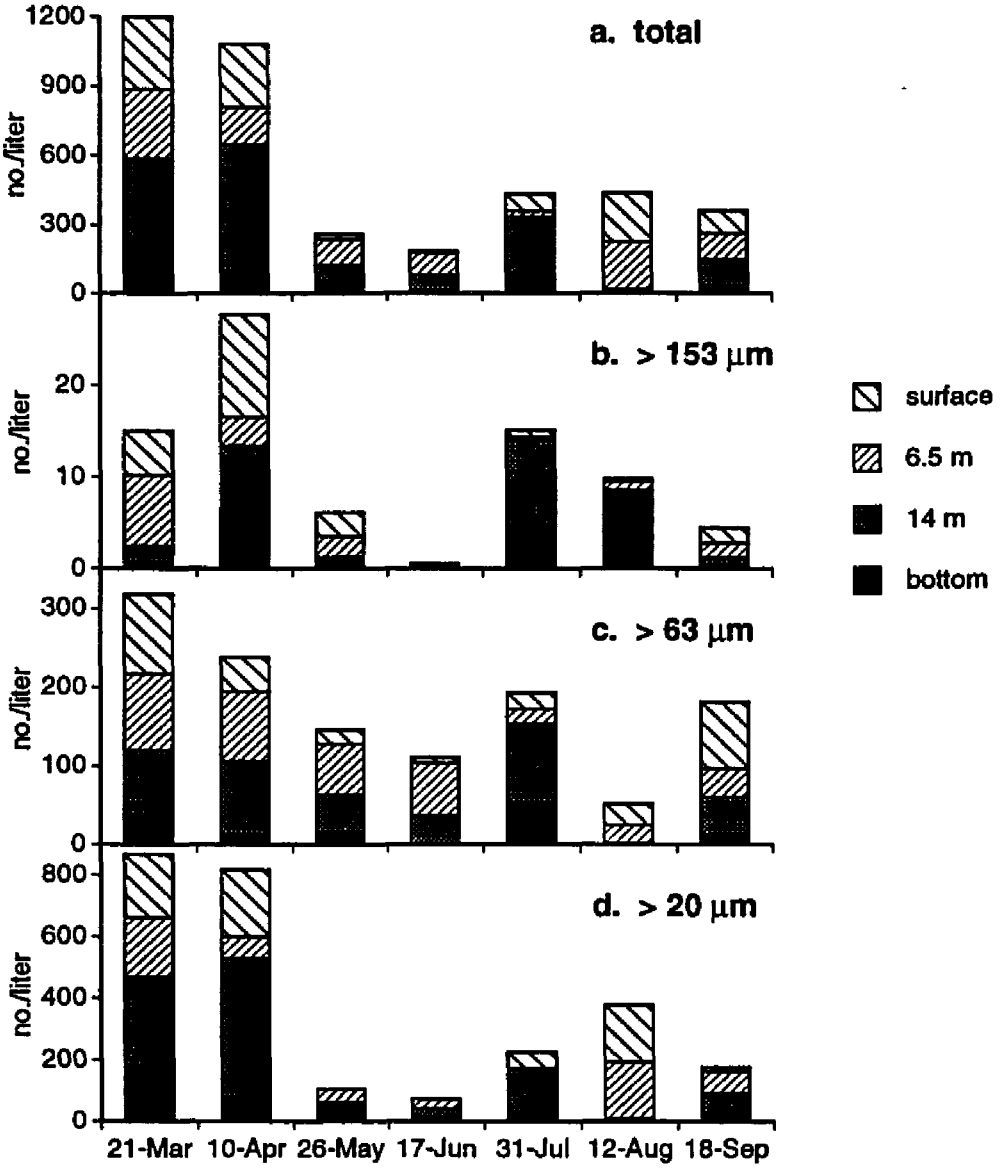


Figure 5.12. Change in concentration of copepod nauplii (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B from March through September 1992.

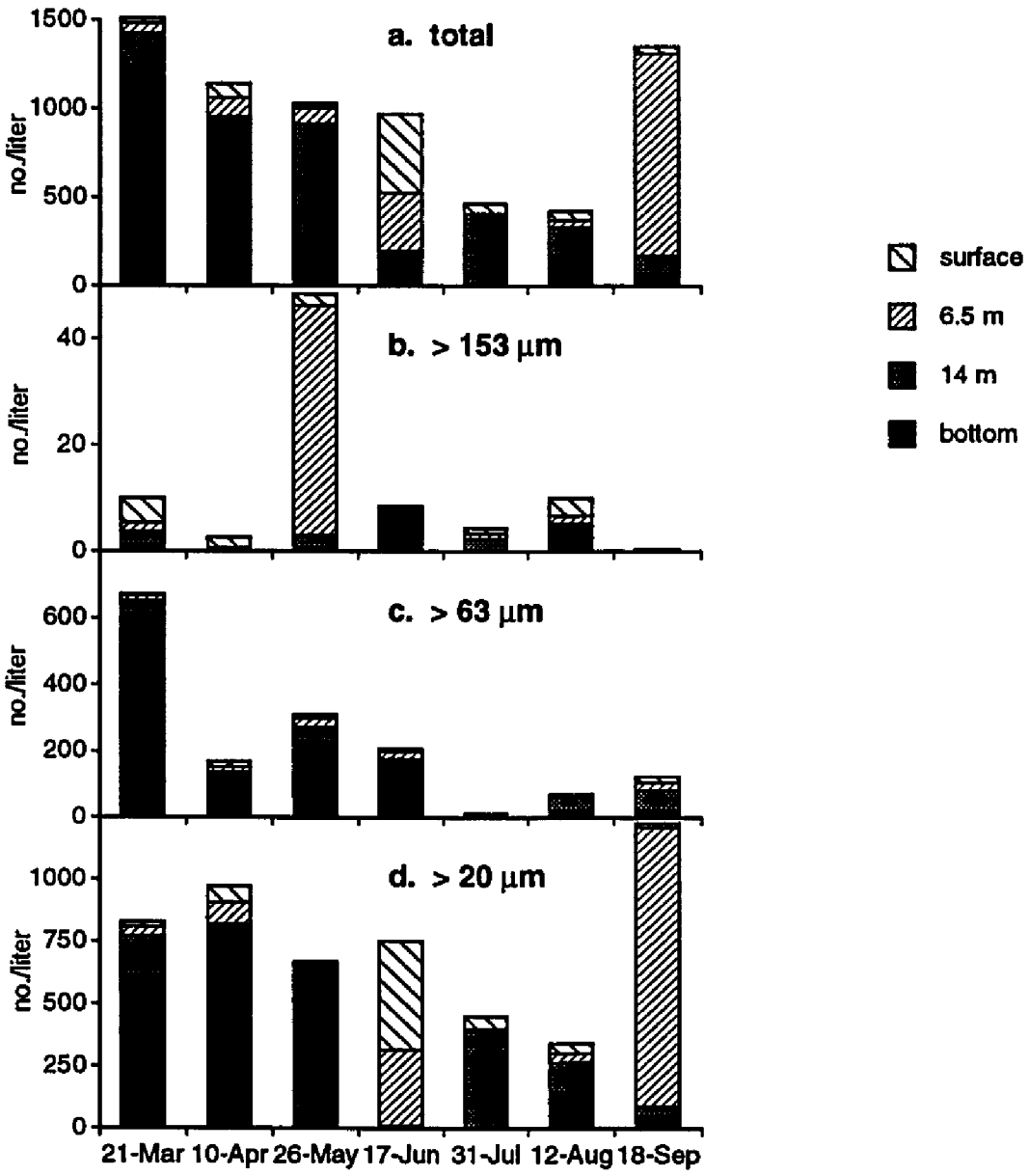


Figure 5.13. Change in concentration of fecal pellets (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions at station C6B from March through September 1992.

correlated with salinity in surface waters, which would represent a higher spring (lower salinities) to lower summer (higher salinities) progression in zooplankton abundances. The number of copepods at 6.5 m were positively related to higher dissolved oxygen and negatively related to lower water temperatures, both conditions more likely in spring. Numbers of total organisms and copepod nauplii at 14 m were positively related to dissolved oxygen and chlorophyll *a* (concentration of food below the pycnocline?) and negatively related to water temperature and salinity (i.e., lower water column conditions during summertime stratification).

Spatial Variability

The samples were collected from varying degrees of bottom waters dissolved oxygen, depths and times, including day and night samples (Table 5.1, Figs. 5.1 and 5.14). The water column was strongly stratified in most cases with a halocline located at 6 to 12 m, depending on the total depth. Gradients in dissolved oxygen paralleled most closely changes in temperature with depth. Bottom waters were oxygenated at station E2, which was the shallowest station.

Mesozooplankton in the > 153 μm size fraction were composed of an average of 45% copepods, ranging from 5 to 80% (Fig. 5.15). More meroplankton were present in the bottom waters at all stations with the exception of stations D6 and C11B; neither station was severely hypoxic and both were in deeper water than the other stations (Table 5.1). Meroplankton contributed 80 to 95% in the lower water column (below pycno-/oxycline and the bottom) at station D2A, a station with severe hypoxia (Fig. 5.15). Copepod nauplii were usually excluded from the lower waters (below pycno-/oxycline and bottom) in the > 153 μm size fraction at stations that were severely hypoxic, but were present in the bottom waters at stations that were less hypoxic to normoxic (Fig. 5.15).

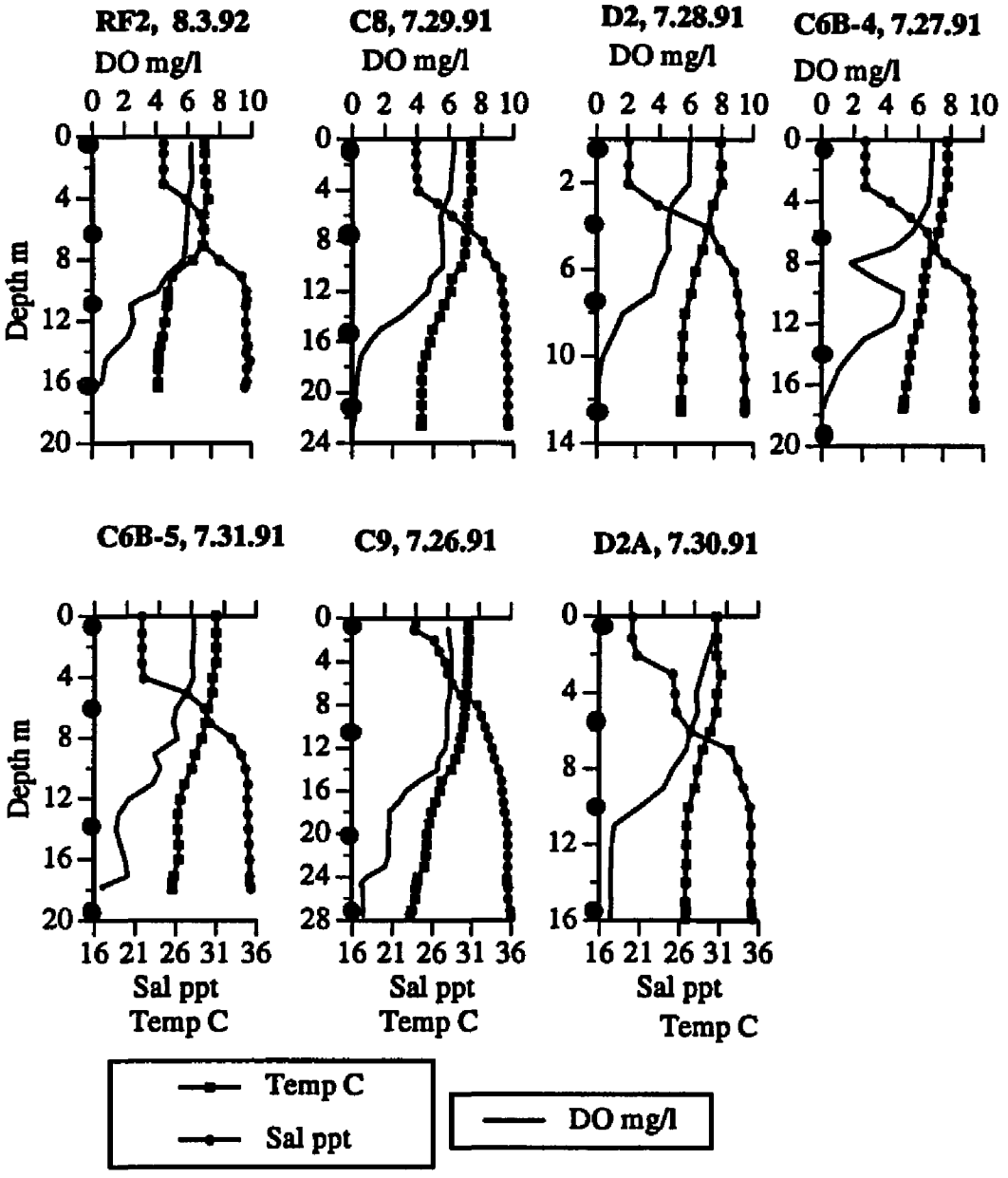
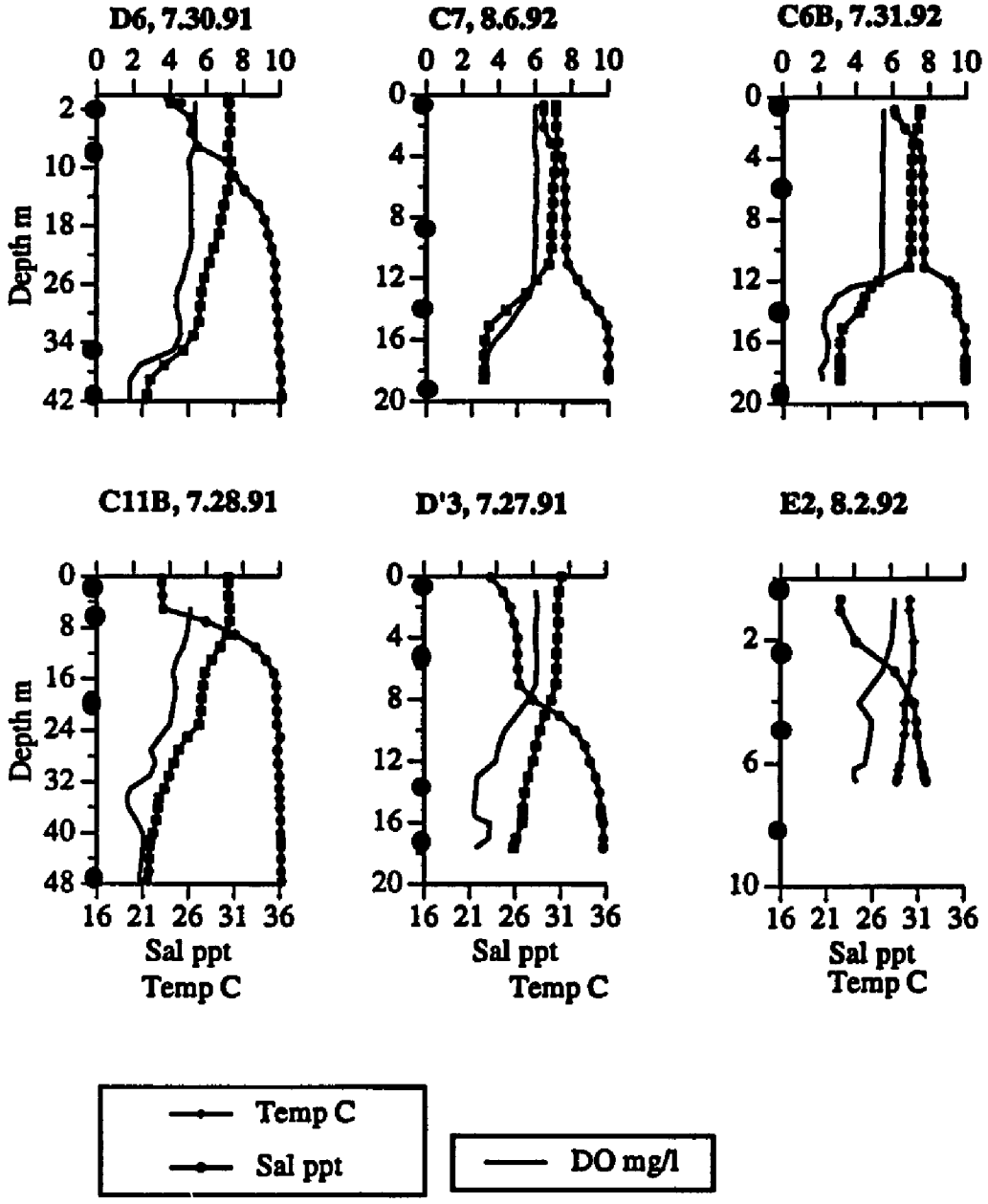


Figure 5.14. Vertical profiles of temperature (degree C), salinity (ppt), and dissolved oxygen (DO mg l^{-1}) for a series of stations with varying concentrations of bottom water dissolved oxygen during two cruises in 1991 and 1992.

(Fig. con'd.)


D6, 7.30.91
C7, 8.6.92
C6B, 7.31.92
C11B, 7.28.91
D'3, 7.27.91
E2, 8.2.92
Depth m
Sal ppt
Temp C
Temp C
Sal ppt
DO mg/l

The concentrations of total organisms were significantly different for all main effects: stations, depths and size fractions (Tables 5.8 and 5.9); the station*depth interaction was also significant. The highest concentration of total organisms was at station D2. The concentration of total organisms was lowest in the bottom waters, but did not appear to be related to day/night differences, but possibly somewhat the severity of hypoxia. More total organisms were present in the upper water column (surface and above pycno-/oxycline) in all size fractions especially at stations with severe hypoxia (Fig. 5.16, Tables 5.8 and 5.9). Station that were not severely hypoxic had more organisms in the lower water column (below pycno-/oxycline and bottom) than severely hypoxic stations (Fig. 5.16).

The copepod concentrations were significantly different for all the main effects: stations, depths and size fractions; the interaction between station*depth and station*size fraction were also significant (Tables 5.8 and 5.9). Copepod concentrations were significantly higher at station D2 than other stations (Table 5.9). Copepods were mostly present in the upper water column (surface and above pycno-/oxycline) with few exceptions (stations C6B-4, C6B-1, C9, C8), where more copepods were present at the bottom layers (below pycno-/oxycline and bottom) (Fig. 5.17). The stations that were the exceptions were sampled during the day, and diel vertical migration by the copepods may have caused the vertical distributions.

The average copepod nauplii concentrations by depth were 62 l^{-1} (± 77) ranging from 1 to 398 l^{-1}. The copepod nauplii concentrations were significantly different for all main effects: stations, depths and size fractions (Tables 5.8 and 5.9); the interactions between station*depth and station*size fraction were also significant. Highest concentrations of copepod nauplii occurred at station D2. Copepod nauplii concentrations followed the trends of total organism concentrations (Fig. 5.18). Most copepod nauplii were present in the upper water column (surface and above pycno-

Table 5.8. Three factorial completely randomized design ANOVA (P>F) for concentration (no. l^{-1}) of total organisms, copepods, copepod nauplii and fecal pellets collected from stations with varying degrees of bottom water dissolved oxygen concentrations during two cruises in late July and August of 1991 and 1992.

	df	Total Organisms P > F	Copepods** P > F	Copepod Nauplii P > F	Fecal Pellets** P > F
Pr < W		0.3334	0.9213	0.9223	0.2861
Model	83	0.0001*	0.0001*	0.0001*	0.0001*
Station	12	0.0066*	0.0001*	0.0002*	0.0009*
Depth	3	0.0002*	0.0275*	0.0001*	0.8288
Size Fraction (SF)	2	0.0001*	0.0001*	0.0001*	0.0001*
Station*Depth	36	0.0001*	0.0001*	0.0001*	0.0046*
Station*SF	24	0.0638	0.0065*	0.0050*	0.0029*
Depth*SF	6	0.9064	0.8334	0.6343	0.0001*

* significant at alpha = 0.05
** log10 transformed data

Table 5.9. Tukey's studentized range test for concentration (no. l^{-1}) of total organisms, copepods, copepod nauplii and fecal pellets collected from stations varying in bottom water dissolved oxygen concentrations on the inner continental shelf during two cruises in late July and August of 1991 and 1992. Means with the same letter are not significantly different (alpha = 0.05).

	Time	Number	Total Organisms* no./ liter	Copepods* no./ liter	Copepod Nauplii* no./ liter	Fecal Pellets* no./ liter
Stations						
RF2	D	12	36.53 ABC	9.89 BC	24.57 BC	21.60 AB
C8	D	12	75.30 ABC	10.02 BCD	47.63 AB	19.35 AB
D2	N	12	264.90 AB	109.50 A	206.88 AB	28.94 A
C6B-4	D	12	38.83 ABC	5.70 E	74.88 ABC	3.45 B
C6B-5	N	12	84.85 ABC	20.24 B	68.68 A	30.21 AB
C9	D	8	31.03 C	7.43 BCDE	22.46 C	20.01 AB
D2A	D	12	104.61 ABC	6.04 CDE	77.54 ABC	32.96 AB
D6	N	12	90.55 ABC	14.97 B	57.06 AB	13.65 AB
C7	N	12	46.20 ABC	5.66 BCDE	45.36 ABC	25.59 AB
C6B-1	D	12	58.66 ABC	14.40 BC	35.99 ABC	38.79 AB
C11B	N	12	35.88 BC	5.27 CDE	29.63 BC	9.54 AB
D'3	N	12	82.79 ABC	2.41 DE	38.87 ABC	26.60 AB
E2	D	12	122.72 A	20.21 B	96.73 AB	4.21 B
Depth						
Surface		37	98.35 A	21.88 AB	65.84 A	13.07 A
Above pycno-/oxycline		37	113.11 A	24.59 A	78.90 A	15.92 A
Below pycno-/oxycline		39	69.97 A	10.50 B	72.06 AB	33.80 A
Bottom		39	56.33 B	11.73 AB	40.76 B	23.38 A
Size Fraction						
>153 µm		52	21.20 B	11.56 B	2.66 B	3.55 C
>63 µm		50	105.60 A	24.66 A	70.50 A	5.64 B
>20 µm		50	127.35 A	0.00	111.17 A	54.08 A

* analysis were performed on log10 transformed data but means are presented as untransformed data
Time: D = day, N = night

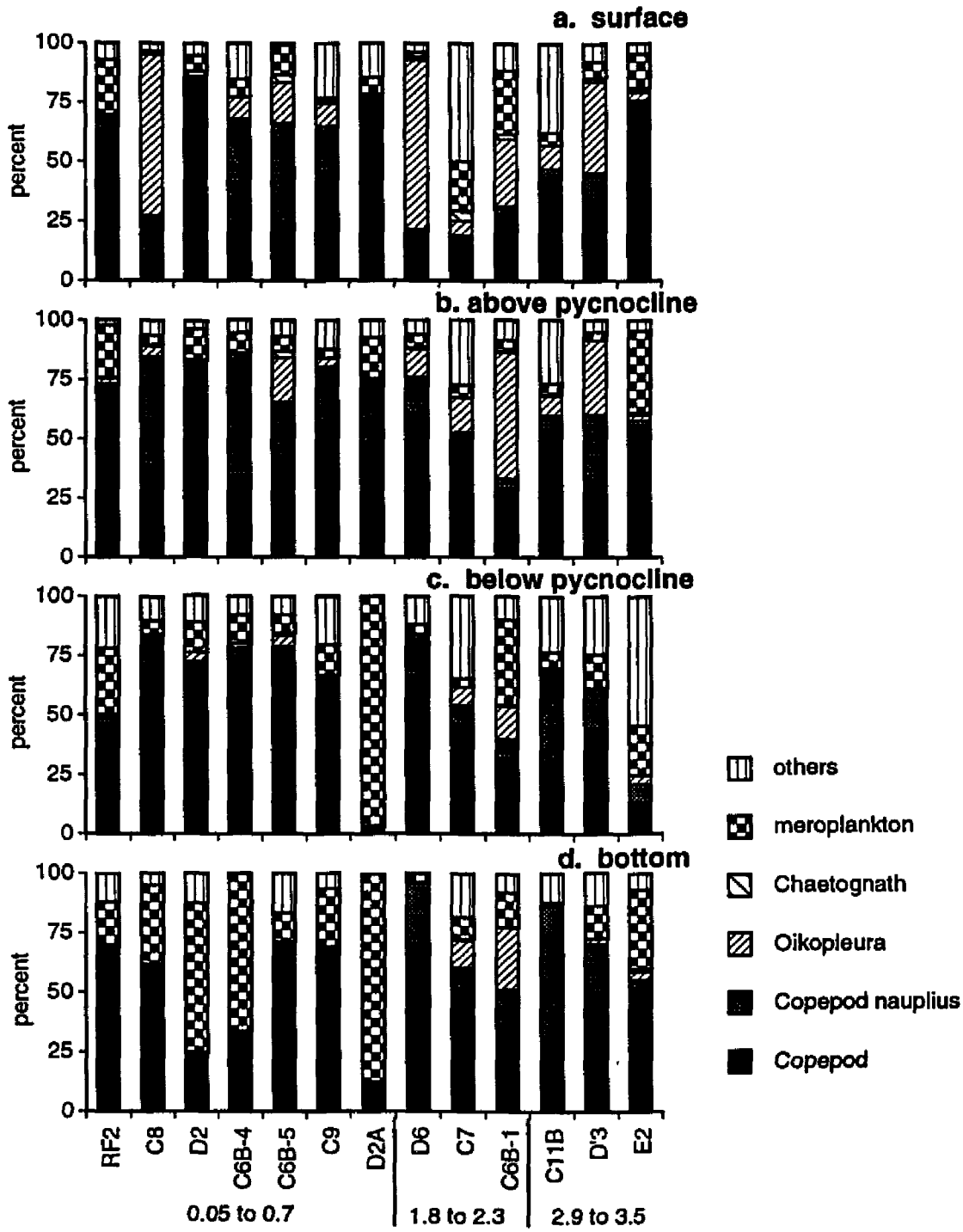


Figure 5.15. Percent composition of mesozooplankton in > 153 µm size fraction at four depths for a series of stations with varying concentrations of bottom water dissolved oxygen during two mid-summer cruises in 1991 and 1992.

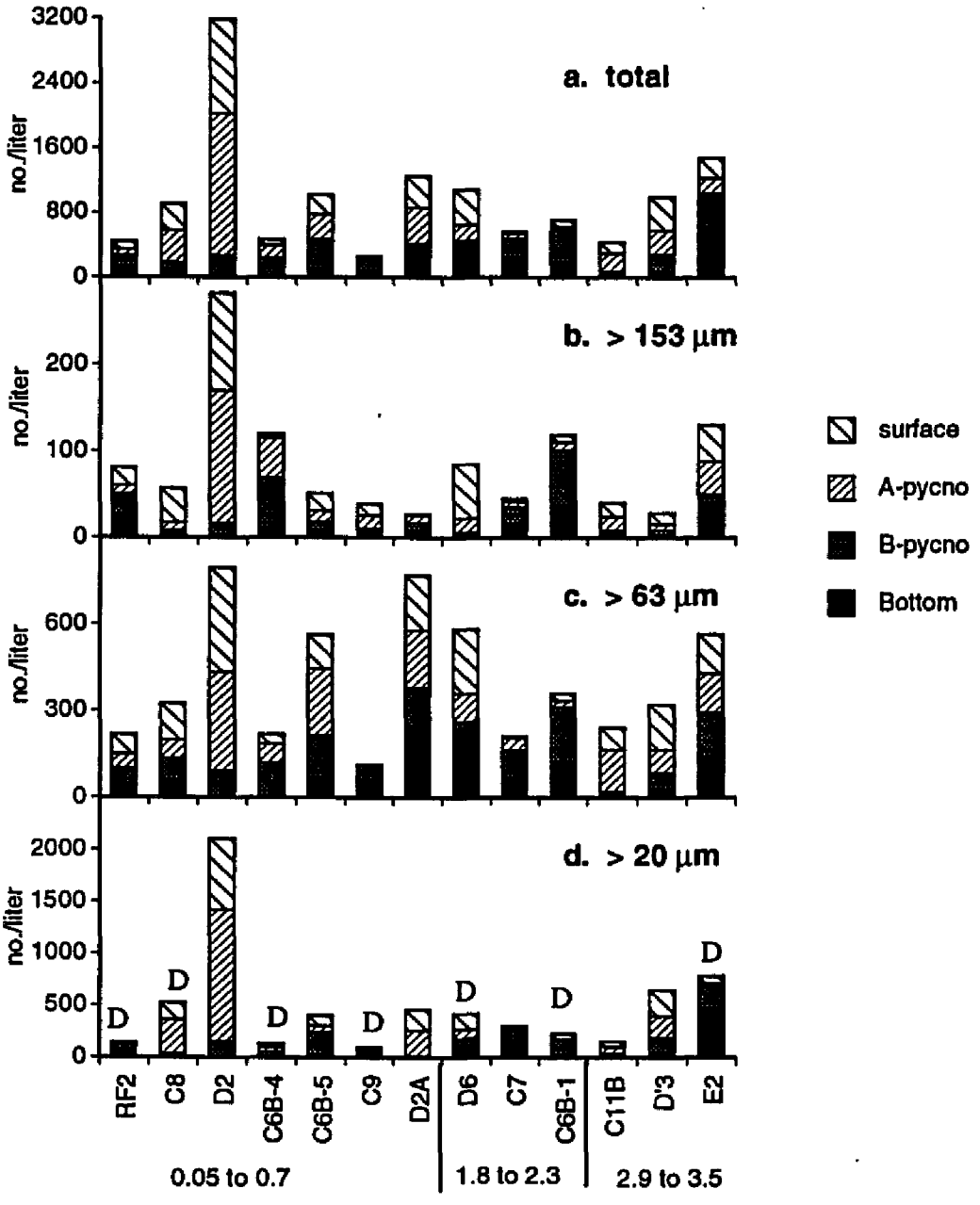


Figure 5.16. Difference in concentration of total organisms (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions for a series of stations with varying concentrations of bottom water dissolved oxygen during two mid summer cruises in 1991 and 1992. (A-pycno = above pycnocline and B-pycno = below pycnocline; D = day)

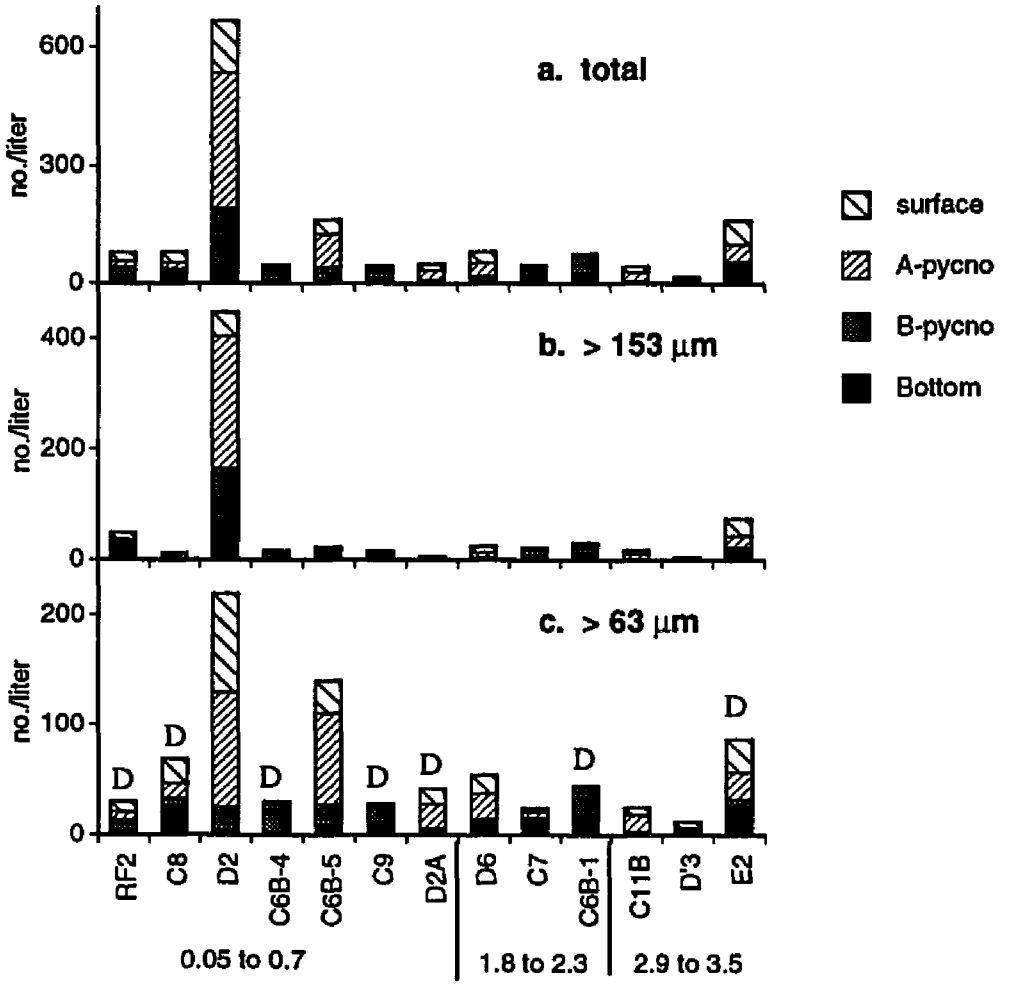


Figure 5.17. Difference in concentration of copepods (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions for a series of stations with varying concentrations of bottom water dissolved oxygen during two mid summer cruises in 1991 and 1992. (A-pycno = above pycnocline and B-pycno = below pycnocline; D = day)

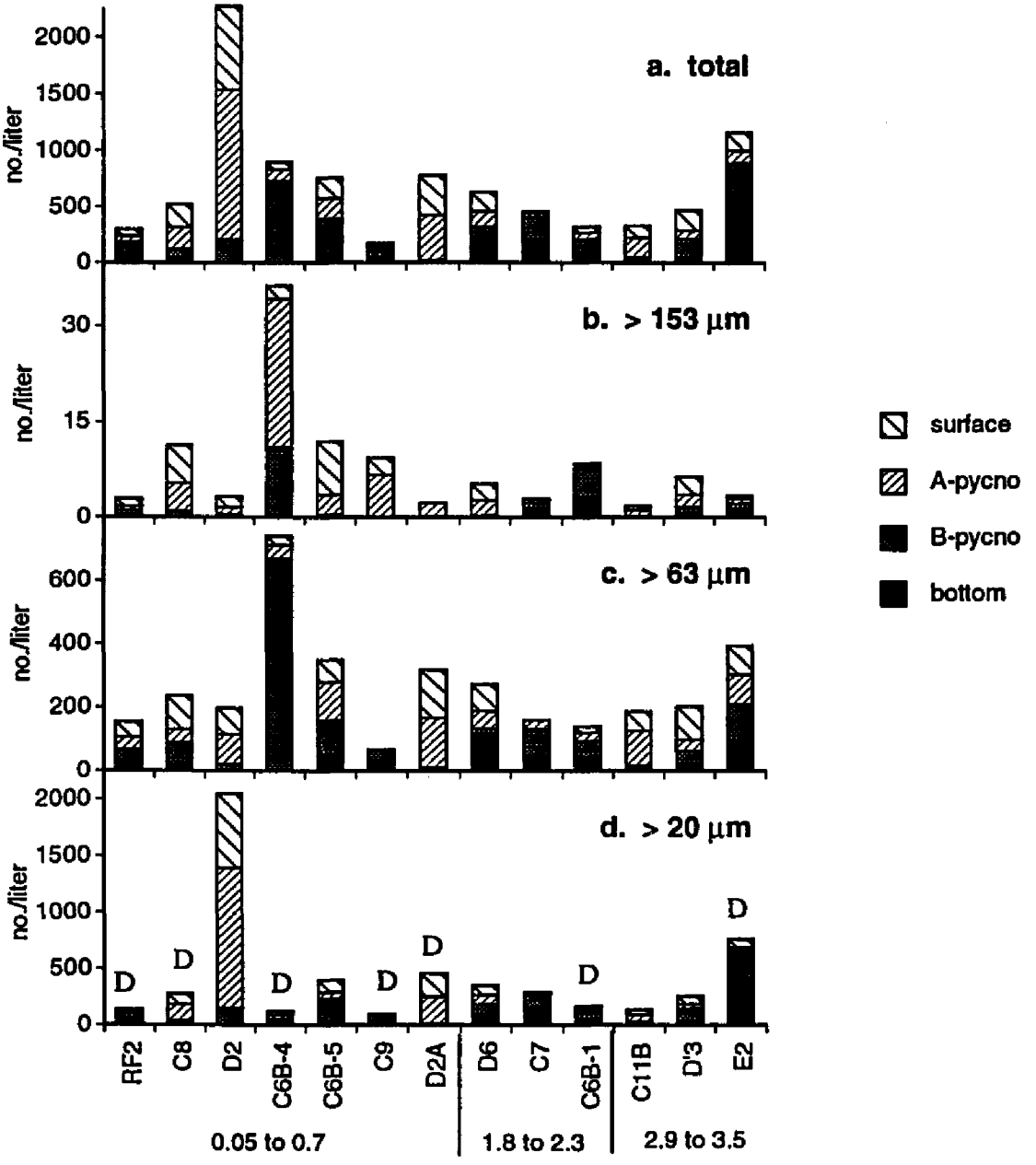


Figure 5.18. Difference in concentration of copepod nauplii (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions for a series of stations with varying concentrations of bottom water dissolved oxygen during two mid summer cruises in 1991 and 1992. (A-pycno = above pycnocline and B- pycno = below pycnocline; D = day)

/oxycline) (Fig. 5.18). More copepod nauplii were present in both the > 63 μm and the > 20 μm size fractions (Fig. 5.18).

Fecal pellet concentrations were significantly different between stations and between size fractions, with a significant interaction term, but not by depth (Table 5.8). Fecal pellet concentrations were high at stations C6B-5 and C6B-1, which were sampled at night. Most fecal pellets were present in the > 20 μm size fraction, and in the lower water column (below pycno-/oxycline and bottom) (Fig. 5.19).

There were positive correlations between total organisms, copepods, copepod nauplii and fecal pellets in the upper water column, surface and above pycno-/oxycline (Table 5.10). There were few positive correlations between the zooplankton constituents and the water column hydrography. This result is not too surprising, since the water column structure was very similar across the study area (few exceptions). Numbers of total organisms and copepod nauplii were positively related to surface water temperature, but this feature varied little, except between day and night. There were negative relationships between organisms, copepods and copepod nauplii and dissolved oxygen and positive relationships with chlorophyll *a* at the above pycno-/oxycline depths. These correlations could represent concentrations of organisms at a subsurface oxygen minimum where food (chlorophyll *a* biomass) is higher. Below pycno-/oxycline numbers of copepods and copepod nauplii showed opposite relationships with dissolved oxygen; the reasons for this are not apparent.

DISCUSSION

The water column was stratified throughout the study period, and the density structure was controlled primarily by salinity. The water column was thermally mixed in March, April and September and at station E2, the shallowest station among those sampled for broad spatial coverage. A strong oxycline existed from March through

Table 5.10. Pearson correlation coefficients matrix showing relationship between concentration (no. l^{-1}) of total organisms, copepods, copepod nauplii and fecal pellets with zooplankton constituents and fecal pellets and ancillary hydrographic data obtained during late July and early August of 1991 and 1992.

	Total Organisms	Copepods	Copepod Nauplii	Fecal Pellets
Surface: n = 14				
Total Organisms	1			
Copepods	0.88 *	1		
Copepod Nauplii	0.97 *	0.87 *	1	
Fecal Pellets	0.72 *	0.64 *	0.76 *	1
Dissolved oxygen (mg/l)	-0.02	-0.08	0.11	-0.23
Salinity (ppt)	-0.38	-0.31	-0.41	-0.21
Temperature (degrees C)	0.54 *	0.48	0.56 *	0.56 *
Chlorophyll a (µg/l)	-0.05	0.18	-0.06	-0.25
Phaeopigment (µg/l)	0.04	0.24	0.01	-0.12
Above pycno-/oxycline: n = 13				
Total Organisms	1			
Copepods	0.66 *	1		
Copepod Nauplii	0.92 *	0.34	1	
Fecal Pellets	0.54 *	0.26	0.46	1
Dissolved oxygen (mg/l)	-0.62 *	-0.87 *	-0.36	-0.13
Salinity (ppt)	-0.07	-0.15	0.01	-0.29
Temperature (degrees C)	0.07	-0.19	0.15	0.35
Chlorophyll a (µg/l)	0.67 *	0.52	0.63 *	0.16
Phaeopigment (µg/l)	0.56 *	0.48	0.51	0.15
Below pycno-/oxycline: n = 13				
Total Organisms	1			
Copepods	0.59 *	1		
Copepod Nauplii	0.34	-0.16	1	
Fecal Pellets	0.46	0.58 *	-0.25	1
Dissolved oxygen (mg/l)	-0.09	-0.52 *	0.54 *	-0.45
Salinity (ppt)	-0.56 *	0.04	-0.47	0.2
Temperature (degrees C)	0.26	-0.02	0.48	-0.54 *
Chlorophyll a (µg/l)	0.5	0.12	0.47	0.64
Phaeopigment (µg/l)	0.5	0.19	0.63 *	0.53
Bottom: n = 13				
Total Organisms	1			
Copepods	0.33	1		
Copepod Nauplii	0.91 *	0.17	1	
Fecal Pellets	0.12	-0.25	-0.13	1
Dissolved oxygen (mg/l)	0.19	-0.21	-0.15	0.79 *
Salinity (ppt)	0.08	-0.02	0.14	-0.04
Temperature (degrees C)	-0.16	-0.01	-0.26	0.23
Chlorophyll a (µg/l)	0.22	0.2	0.29	-0.25
Phaeopigment (µg/l)	-0.27	-0.22	-0.19	-0.21

* significant at alpha = 0.05

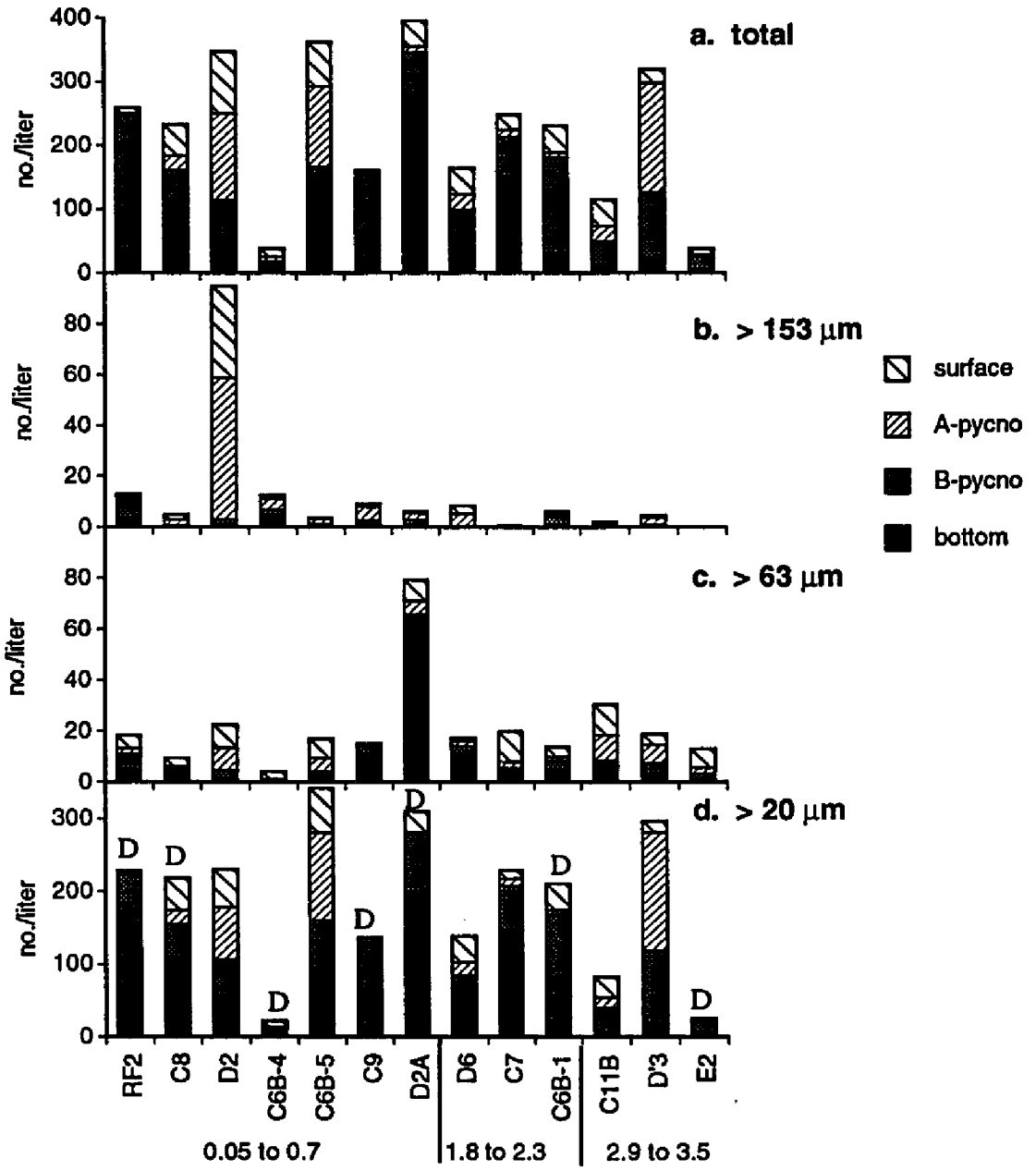


Figure 5.19. Difference in concentration of fecal pellets (no. l^{-1}) at four depths for size fractions indicated and total of all size fractions for a series of stations with varying concentrations of bottom water dissolved oxygen during mid summer two cruises in 1991 and 1992. (A-pycno = above pycnocline and B-pycno = below pycnocline; D = day)

August, but not in September. Sampling in September occurred after the passage of Hurricane Andrew and the passage of several cold fronts. Spatial and diel variability data were collected in late July and early August when the water column was strongly stratified at station C6B as well as most other stations.

The nested filtration through different mesh sizes isolated organisms according to size classes. Mesozooplankton were present in the > 153 μm size fraction, and were the most diverse there, with the dominant groups of organisms including copepods, copepod nauplii, oikopleurans, meroplankton (mostly included benthic larvae), chaetognaths and others (medusae, amphipods, cladocerans, ostracods, doliolids, and fish larvae and eggs). The > 63 μm and > 20 μm size fractions usually retained microzooplankton of which only copepod nauplii were counted. Fecal pellets were isolated according to size, and most were collected in the > 20 μm size fraction.

Diel Variability

The diel vertical migration of zooplankton has long been recognized and various groups such as copepods, chaetognaths, euphausiids, medusae, and fishes undergo diel vertical migration. This migration is usually influenced by exogenous (light, gravity, oxygen, food, predation) and or endogenous (biological rhythms) factors (Andersen & Nival 1991). Diel vertical migration can influence the downward flux of particulate organic material (Angel 1984, Fowler & Knauer 1986, Turley 1992). Zooplankters act as 'biological pumps', by feeding in surface layers and defecating at depth, thus accelerating the fecal pellet flux to the benthos (Walsh et al. 1988, Dagg & Walser 1987, Longhurst & Harrison 1988, Turley 1992).

The water column was highly stratified and did not change over the 24-h sampling at station C6B. Bottom water dissolved oxygen levels fluctuated around 2 mg l^{-1}. Most of the organisms were copepod nauplii, but a high percentage of copepods was also present. Highest numbers of all organisms, including copepods and

copepod nauplii, occurred at 16:30, and they were concentrated in the lower water column. Copepod nauplii moved up into the water column at 23:30 and were more evenly distributed across all depths, but copepods remained in the lower water column. The copepod nauplii moved back into the lower water column at 06:15, which is where the copepods remained concentrated. Numbers of organisms were extremely low at 10:05, but evenly distributed in the water column. Thus, copepod nauplii migrated into the upper water column at night and remained in the lower water column during the day, while the copepods were concentrated in the lower water column for the full 24-h period. Bottom water oxygen concentrations were not stressful and did not disrupt diel vertical migration (*sensu* Chesapeake Bay results, Roman et al. 1993).

There number of organisms were lowest at 10:05 (1 h before apparent noon) in all size fractions. The low density of organisms collected then might be related to avoidance of sampling gear (Niskin bottle). Bishop et al. (1987) reported > 60% of the copepods in the upper 100 m water column avoided gear (a Large Volume Filtration System used in comparison to samples collected by a MOCNESS (Wiebe et al. 1976)).

Copepods stayed in the lower water column (14 m and bottom) and did not vertically migrate over 24 hours. Swarms of *Acartia* have been reported close to the bottom, and the reasons for this behavior are not clearly understood (Kimoto et al. 1984). An investigation of *Acartia tonsa*'s vertical migratory behavior in response to food patchiness showed an ability to remain within thin food layers and produce fecal pellets as in homogeneous food conditions (Tiselius 1992). Copepods reduced feeding activity, but still stayed in the patch.

Fecal pellet concentrations were highest at 16:30 and in the lower water column (more at 14 m depth). Also, the abundance of fecal pellets was related to the numbers of total organisms, copepods and copepod nauplii. The number of fecal pellets has been used as an index of grazing intensity, and reflects the influence of food concentration and feeding rates (Haney & Trout 1990). The organisms in the lower

water column were the likely producers of the fecal pellets collected there. Entrainment of particles at the density gradient may result in feeding activity at that depth so that more fecal pellets were accumulating below the pycnocline where organisms were feeding. Feeding on entrained particles near a density interface has been reported from various regions (Walsh et al. 1988, Gardner 1989, Youngbluth et al. 1989). Jackson (1993) proposed the concept of flux feeders (larvaceans, pteropods, and copepods) residing below the euphotic zone and likely controlling carbon recycling by intercepting sinking particles. These flux feeders are also likely producing fecal pellets in the lower water column. The significant positive correlations between the concentration of fecal pellets and densities of total organisms, copepods and copepod nauplii, over the 24-h period indicates that fecal pellets were produced by copepod and copepod nauplii, and the fecal pellets were likely freshly produced and were at a recognizable state and were not disintegrated remineralized and recycled by copepods or other mesozooplankton.

Monthly Variability

The water column was strongly stratified with a strong oxycline throughout the study period, except in September. The total number of organisms was dominated by copepod nauplii, but a high percentage of copepods occurred in the samples as well. The total organisms, either copepod nauplii or copepods, were highest in March and April. There was a seasonal decline in summer and into fall. The negative correlation of abundances with surface water salinity parallels the progression from a spring high (lower salinities) to summer and fall lows (higher salinities). The seasonal trend is also related to the food availability in the surface waters (i.e., higher chlorophyll *a* biomass in spring and much lower values in summer and fall, Fig. 2.8). The most severely oxygen deficient bottom waters occurred in June and August; numbers of organisms

were most reduced in the lower water column during those two collections with the exception of copepods at 14 m in August.

Copepod and copepod nauplii concentrations averaged 33 l^{-1} and 135 l^{-1}, respectively over the study period. Copepod nauplii abundances were highest in March and April (approximately 100 l^{-1} in both months). Naupliar densities in this study exceeded those reported by Dagg et al. (1987) for the Mississippi River delta in spring and winter, as well as those reported from stations very near C6B in April 1988 (Dagg and Whitledge 1991).

The total fecal pellet concentrations were higher in the bottom waters (but not significantly) and were positively correlated with numbers of copepod nauplii. More smaller fecal pellets in the > 20 μm size fraction and a high copepod nauplii density in the > 20 μm size fraction indicated that copepod nauplii were the likely producers of the smaller fecal pellets. Concentration of fecal pellets in the lower water column was similar to the results of the diel study. An exception to this was the presence of more fecal pellets at 6.5 m in September, which was likely related to higher abundances of copepod nauplii in the upper water column. High fecal pellet flux into the top trap in fall (Table 2.3, Fig. 2.9) paralleled the high concentration of fecal pellets in the upper water column in September. Similarly, higher fluxes of fecal pellets into the sediment traps occurred in spring, when microzooplankton abundances were higher. Some other possible explanations for concentration of fecal pellets in the lower water column include higher feeding activity near the pycnocline (as discussed for diel variability), as well as possible resuspension of fecal pellets (Chapter 2).

Effect of Hypoxia on the Distribution of Zooplankton

The positive correlations of total organisms and copepod nauplii with dissolved oxygen in the lower water column in the monthly collections (but not the diel and spatial, because of uniformity of water column characteristics) indicated that higher

densities of organisms would occur in more oxygenated waters and/or organisms would avoid bottom waters low in dissolved oxygen. Organism abundances (except for copepods at 14 m) were extremely low in the bottom water column in June and August when hypoxia was most severe and extended 3 m and 7 m above the bottom, respectively. Low oxygen concentrations paralleled reduced copepod abundances in the mesohaline region of Chesapeake Bay, and densities of copepods increased with an increase in oxygen in the bottom waters (Roman et al. 1993).

Roman et al. (1993) demonstrated that *Acartia tonsa* is more limited in its ability to survive low oxygen concentration compared to *Oithona colcarva*. Apparently, a low respiration rate and metabolism (Lampitt & Gamble 1982) enables *Oithona* to survive low oxygen conditions more easily. Roman et al. (1993) also observed the displacement of copepod nauplii into the surface waters, concentration of copepod eggs into the thermocline area and inhibition of copepod egg hatching at dissolved oxygen < 1mg O_2 l^{-1}. The inhibition of hatching in low oxygen would likely reduce recruitment of copepods. The idea that reduced abundance of copepods in the mesohaline region of Chesapeake Bay in May, which was previously suggested to be related to ctenophore predation on the copepod standing stocks, was rejected by a recent predation study (Purcell et al. 1994). Purcell et al. (1994) found no limitation on abundance of *Acartia tonsa* due to predation by gelatinous zooplankton. However, a decrease in oxygen concentration correlated with a decrease in abundance of copepod nauplii could be explained by an inhibition in hatching of copepod eggs under low oxygen conditions and an ultimate reduction in copepod recruitment (Roman et al. 1993). It is very likely that more than one factor influences zooplankton distribution in the stratified water column under the influence of hypoxic bottom waters. A combination of factors: food availability, predation, and low-oxygen bottom waters may act synergistically to reduce copepod abundance in summer months (Roman et al. 1993), and would also influence the amount of carbon flux.

Meroplankton, which included mostly benthic larvae: polychaete larvae, balanoglossus larvae, pilidium larvae of nemerteans, and ophiopleuteus (brittle star larvae) were present. The presence of a high percentage of meroplankton in the lower water column, especially during severe hypoxia (June and August) indicated that these larvae either delayed their settlement or were not able to settle due to unfavorable environmental conditions.

Spatial Variability

The percent contribution to the total in the > 153 μm size fraction showed greater percentage of meroplankton in the lower water column at stations with severely delpeted bottom water dissolved oxygen (Fig. 5.15), similar to the results of the monthly collections during severe hypoxia. Although copepods were present in the bottom waters at all stations and at all depths, copepod nauplii were not present in the lower water column at stations that were severely depleted in bottom water depletion (Station RF2 to D2A in Fig. 5.15).

Station D2 (severely hypoxic) had the highest densities of total organisms, copepods, copepod nauplii in the upper water column (surface and 6.5 m). This might be due to displacement of organisms from severely hypoxic bottom waters. Secondly, this station was sampled at night, and zooplankton may have migrated into surface waters for feeding. The distributions of total organisms, copepods, copepod nauplii and fecal pellets were significantly different across the broad area of bottom water dissolved oxygen cencentrations, but there were no significant differences in abundances over a continum of bottom water dissolved oxygen concentrations. However, most of the organisms were present in the upper water column in almost all stations and in all size fractions, with a few exceptions when copepods were present in the lower water column. The concentrations of total organisms, copepods and copepod nauplii were evenly distribution at all depths at stations where bottom water oxygen concentrations

varied from 1 to 3 mg l^{-1}. More displacement of organism into the upper water column occurred when the lower water column was severely hypoxic. Dagg et al. (1987) observed aggregations of copepod nauplii in upper layers at stations that very strongly physically stratified and homogeneous vertical distributions at stations lacking physical stratification.

The number of fecal pellets were positively correlated with the abundances of total organisms, copepods and copepod nauplii, which indicates that these organisms are the likely source. This result is consistent with the diel and monthly collections.

CONCLUSIONS

The influence of Mississippi-Atchafalaya riverine inputs is seen in stratified, highly productive coastal waters. The vertical stability and high organic load depletes bottom water oxygen, and hypoxic bottom water prevails much of the year. In a stratified water column where oxygen depletion is severe, any shift in the abundance and distribution of zooplankton can have direct and indirect effects on carbon flux. The distribution of meso- and microzooplankton and fecal pellets was determined on a monthly and diel scale of variability at station C6B, and on a broad spatial scale across a variety of stations in mid-summer over a continum of bottom water dissolved oxygen concentrations.

Copepod nauplii migrated into the upper water column at night and remained in the lower water column during the day, while the copepods remained concentrated in the lower water column for the full 24-h period. Bottom water oxygen concentrations were not stressful during the 24-h collections and did not disrupt diel vertical migration. Highest densities of total organisms, copepods and copepod nauplii occurred during March and April when chlorophyll *a* concentrations in the upper water column were highest and decreased in summer and fall when food resources were reduced. Other

possible mechanisms for reduced zooplankton abundances are increased predation, reduced habitat (i.e., oxygen deficient bottom waters), inhibition of copepod egg hatching in oxygen depleted bottom waters and reduced copepod recruitment. The positive correlations of total organisms and copepod nauplii with dissolved oxygen in the lower water column in the monthly collections indicated that higher densities of organisms would occur in the more oxygenated waters and/or organisms would avoid bottom waters low in dissolved oxygen. Within the stations sampled across the hypoxic zone in mid-summer, there were no significant differences in abundances between stations which varied over a continuum of bottom water dissolved oxygen concentrations. Although copepods were present in the bottom waters at all stations and at all depths for the spatial survey, copepod nauplii were not present in the lower water column at stations that were severely hypoxic.

The number of fecal pellets were positively correlated with the abundances of total organisms, copepods and copepod nauplii, which indicated that these organisms are the likely source. Similarities were observed between the seasonal pattern of meso- and microzooplankton and the flux of fecal pellets into the moored sediment traps at station C6B. High fecal pellet flux into the top trap in fall paralleled the high concentration of fecal pellets in the upper water column in September. Similarly, higher fluxes of fecal pellets occurred into the sediment traps in spring, when microzooplankton abundances were higher.

REFERENCES

ANDERSEN, V., AND P. NIVAL. 1991. A model of diel vertical migration of zooplankton based on euphausiids. J. Mar. Res. **49**: 153-175.

ANGEL, M. V. 1984. Detrital organic fluxes through pelagic ecosystems. p. 475-516. *In* M. J. R. Fasham [ed.], Flow of energy and material in marine ecosystems. NATO Conference Series V. Marine Science 13. Plenum.

BATHMANN, U. V., T. T. NOJI, M. VOSS, AND R. PEINERT. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Mar. Ecol. Prog. Ser. **38**: 45-51.

BISHOP, J. K., J. C. STEPIEN, AND P. H. WIEBE. 1987. Particulate matter distributions, chemistry and flux in the Panama Basin: response to environmental forcing. Prog. Oceanogr. **17**: 1-59.

DAGG, M. J., AND W. E. WALSER JR. 1986. The effect of food concentration on fecal pellet size in marine copepods. Limnol. Oceanogr. **31**: 1066-1071.

_____, AND _____. 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. Limnol. Oceanogr. **32**: 178-188.

_____, AND T. E. WHITLEDGE. 1991. Concentrations of copepod nauplii associated with the nutrient rich plume of the Mississippi River. Cont. Shelf Res. **11**: 1409-1423.

_____, AND P. B. ORTNER. 1992. Mesozooplankton grazing and the fate of carbon in the northern Gulf of Mexico. p. 117-121. *In*: Proceedings, NECOP Synthesis Meeting, Publ. NO. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, _____. 1993. Grazing by meso- and micro-zooplankton in plume waters of the Mississippi and Atchafalaya Rivers. p. 27-29. *In* S. E. Lohrenz (ed.) Proceedings of the 1993 NECOP Data Workshop. University of Southern Mississippi, Gulf Coast Campus. Long Beach, Mississippi.

_____, P. ORTNER, AND F. AL-YAMANI. 1987. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. Fish. Bull. **86**: 319-330.

FOWLER, S. W., AND G. A. KNAUER. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. **16**: 147-194.

GARDNER, W. D. 1989. Baltimore Canyon as a modern conduit of sediment to the deep sea. Deep-Sea Res. **36**: 323-358.

HANEY, J. F., AND M. A. TROUT. 1990. Relationships between fecal pellet production and feeding in the calanoid copepod *Boeckella*. J. Mar. Res. **12**: 701-716.

JACKSON, G. A. 1993. Flux feeding as a mechanism for zooplankton grazing and its implications for vertical particulate flux. Limnol. Oceanogr. **38**: 1328-1331.

JUSTIC', D., N. N. RABALAIS, R. E. TURNER, AND W. J. WISEMAN JR. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. Mar. Pollut. Bull. **26**: 184-189.

KEMP, W. M., P. A. SAMPOU, J. GARBER, J. TUTTLE, AND W. R. BOYNTON. 1992. Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: roles of benthic and planktonic respiration and physical exchange processes. Mar. Ecol. Prog. Ser. **85**:137:152.

KIMOTO, K., J. NAKASHIMA, AND Y. MORIOKA. 1988. Direct observations of copepod swarm in a small inlet of Kyushu, Japan. Bull. Seikai Reg. Fish. Res. Lab. **66**: 41-55.

LONGHURST, A. G, AND W. G. HARRISON. 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. **35**: 881-889.

PILSKALN, C. H., AND S. HONJO. 1987. The fecal pellet fraction of biogeochemical particle fluxes to the deep sea. Global Biogeochem. Cycles **1**: 31-48.

PURCELL, J. E., J. R. WHITE, AND M. R. ROMAN. 1994. Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. Limnol. Oceanogr. **39**: 263-278.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. p. 35-47. *In* Tyson, R. V. and T. H. Pearson [eds.] *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication No. 58, The Geological Society, London.

_____, _____, AND _____. 1992. Distribution and characteristics of hypoxia on the Louisiana shelf in 1990 and 1991. p. 15-20. *In*: Proceedings, NECOP Synthesis Meeting, Publ. NO. TAMU-SG-92-109, Texas Sea Grant College Program, College Station, Texas.

_____, _____, AND _____. 1994a. Hypoxia conditions in bottom waters on the Louisiana-Texas shelf. Pages 50-54. *In* M. J. Dowgiallo (ed.), Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding, Special NOAA Report, National Oceanic and Atmospheric Administration, Coastal Ocean Office, Silver Spring, Maryland.

_____, W. J. WISEMAN, JR., AND R. E. TURNER. 1994b. Comparison of continuous records of near bottom dissolved oxygen from the hypoxic zone of Louisiana. Estuaries **17**:

RILEY, G. A. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. J. Mar. Res. **1**: 60-83.

ROMAN, M. R., A. L. GAUZENS, W. K. RHINEHART, AND J. R. WHITE. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. Limnol. Oceanogr. **38**: 1603-1614.

SAS INSTITUTE. 1985. SAS User's Guide: Statistics, Version 5 edition. SAS Institute Inc., North Carolina, 956 p.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and Procedures of Statistics. McGraw Hill.

SUESS, E. 1980. Particulate organic carbon flux in the ocean -- surface productivity and oxygen utilization. Nature **288**: 260-263.

TISELIUS, P. 1992. Behavior of *Acartia tonsa* in patchy food environments. Limnol. Oceanogr. **37**: 1640-1651.

TURLEY, C. M. 1992. Formation, vertical flux and remineralization of aggregates in the ocean: a short review. Arch. Hydrobiol. Beih. Ergebn. Limnol. **37**: 155-163.

WALSH, I., J. DYMAND, AND R. COLLIER. 1988. Rates of recycling of biogenic components of settling particles in the ocean derived from sediment trap experiments. Deep-Sea Res. **35**: 43-58.

WIEBE, P. H., S. H. BOYD, AND C. WINGET. 1976. Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean, Bahamas, with a description of a new sedimentation trap. J. Mar. Res. **34**: 341-354.

YOUNGBLUTH, M. J., T. G. BAILEY, P. J. DAVOLL, C. A. JACOBY, P. I. BLADES-ECKELBARGER, AND C. A. GRISWOLD. 1989. Fecal pellet production and diel migratory behavior by the euphausiid *Meganyctiphanes norvegica* effect benthic-pelagic coupling. Deep-Sea Res. **36**: 1491-1501.

CHAPTER 6

CONCLUSIONS

The influence of Mississippi-Atchafalaya riverine inputs is seen in stratified, highly productive coastal waters. The vertical stability and high organic load depletes bottom water oxygen, and hypoxic bottom water prevails much of the year. In this framework, I hypothesized that zooplankton fecal pellet carbon was the primary source of carbon to the seabed. In this study, I examined the temporal variability of fecal pellet and fecal pellet carbon fluxes and evaluated the contribution of fecal pellet carbon to the total carbon flux and determined the potential of fecal pellets to oxidize and induce hypoxia. The data set, covering over two years (approximately 66 to 70% of each year), and obtained from the long-term deployment of sediment traps moored at a permanent station (C6B) in the core of the hypoxic region increased understanding of the temporal variation in the production exported to the seabed on the inner continental shelf under the influence of the Mississippi-Atchafalaya system. In a stratified water column where oxygen depletion is severe, physical and biological processes directly or indirectly affect the flux of carbon, and any shift in the abundance and distribution of zooplankton communities can have direct and indirect effects on carbon flux.

There was considerable inter-annual and temporal variability in the fecal pellet number and carbon flux. I hypothesized that the summertime flux of fecal pellets would exceed that of spring and summer, because a mature zooplankton population would be likely to produce larger fecal pellets that would sink quickly from the upper layers. Instead, carbon fluxes as fecal pellets ranged from 1.5 to 4818 mg C m^{-2} d^{-1}, were highest in the spring and lowest in the summer with fall being intermediate. Although statistically not significant, both fecal pellet and fecal pellet carbon fluxes were higher in 1991 than in 1992. More fecal pellets were collected in the bottom trap

compared to the top trap. The deposition rates of fecal pellets collected in the top and bottom traps ranged from $1.5*10^4$ to $4.7*10^6$ m^{-2} d^{-1} , and from $2.1*10^4$ to $2.2*10^7$ m^{-2} d^{-1} respectively. More smaller than larger fecal pellets were collected at both depths. The highest fecal pellet carbon flux, however, was accounted for by the larger pellets.

More fecal pellets were collected in the bottom trap compared to the top trap, which is likely due to depth integration, zooplankton feeding on the particles entrained at the pycnocline, zooplankton acting as 'biological pumps', and/or collection of resuspended material in the bottom trap. Fecal pellet carbon flux was dominated by larger particles, as I had predicted, but the percentage of smaller fecal pellets exceeded that of the larger size fraction.

The size and shape of fecal pellets collected in the sediment traps and knowledge of the meso- and microzooplankton communities in the study area (Chapters 4 and 5) indicated that the fecal pellets in the traps were likely produced by the dominant zooplankters, copepods and larvaceans. The smaller fecal pellets were more in number but the mid-sized, ellipsoidal fecal pellets were probably an important component of fecal pellet carbon flux. Larger, tubular fecal pellets, however, were occasionally abundant and periodically influenced the carbon flux values.

Comparison of the flux data with water column hydrographic data indicated that fecal pellet carbon flux was greater during periods of higher surface water production (as indicated by high dissolved oxygen and pigment concentrations). Higher fecal pellet carbon flux in 1991 compared to 1992 can also be linked to productivity in the surface waters since the spring freshet of the Mississippi River was much greater in 1991 than in 1992. The number and carbon flux of fecal pellets in the spring are likely directly related to food availability and high phytoplankton biomass stimulated by the nutrient rich Mississippi River waters.

The negative relationship between fecal pellet and fecal pellet carbon fluxes with delta sigma t indicates less flux during periods of greatest stratification (i.e. summer) and higher fluxes during periods when the water column was mixed. Lower fluxes in summer may be due to reduced zooplankton abundance, food availability, retention or remineralization of fecal pellets in the upper water column, or reduced potential of resuspension in the absence of spring and fall mixing events. The higher values in spring, compared to fall, although resuspension might occur during both seasons, are more likely related to greater food availability. Phytoplankton biomass in the surface waters is generally higher in spring than in fall.

Further evidence for seasonal differences in flux through the water column was seen in the seasonal differences in fecal pellet carbon in the surficial sediments. Both spring and summer sediment fecal pellet carbon were much higher than in the fall. Summertime accumulation of fecal pellets in the surficial sediments was facilitated by minimal bottom currents, although fecal pellets could be resuspended from the sediment surface. Resuspension of fecal pellets would likely occur for a large portion of mid-summer 1992 based on calculations of critical velocity from a limited current meter record. Larger fecal pellets dominated the surficial sediments, possibly due to winnowing of smaller fecal pellets or selective utilization by benthic organisms.

The average fluxes of total particulate material (TPM), particulate organic carbon (POC) (Chapter 3) and fecal pellet carbon (FPC) (Chapter 2) were high compared to other coastal regions. Highly significant and positive correlations between TPM, POC, PON (particulate organic carbon), total pigment and FPC fluxes in both the top and the bottom traps indicated that sedimentation rates of the components were related to each other. These results also demonstrated the importance of surface waters as a source of material sedimented into both traps. The flux of TPM, POC, PON, FPC, P_{cell} (phytoplankton carbon flux) and total pigments varied similarly between seasons, with lowest sedimentation in summer. There were also inter-annual differences, with

1991 fluxes (except P_{cell} which was not calculated for 1992) exceeding those of in 1992. Higher fluxes of TPM into the bottom traps, especially in the fall, were most likely the result of sediment resuspension, as determined from dilution of the trap materials with sedimentary %TOC and C:N ratios. Similar to FP and FPC fluxes, surface fluxes were positively correlated with indicators of high surface water production (dissolved oxygen and pigment concentrations) for the 1991 series, but not for 1992. High surface water production occurs in spring, and the yearly differences in the strength of relationships to indicators of surface water productivity can be related to the differences in the spring freshet of the Mississippi River, which was much greater in 1991 than in 1992. Fluxes of most bottom trap materials were positively correlated with the lower water column dissolved oxygen (i.e. mixed water column) and negatively correlated with the lower water column salinity (i.e. stratified water column). These results indicate that a decrease in the export of primary productivity was related to density structure and low export ratios were seen in summer when the water column was highly stratified.

The greatest potential for sinking of organic material derived from *in situ* production exists in the spring when riverine nutrient delivery stimulates increased phytoplankton production. The export of carbon from surface waters to the lower water column and sediments on the southeastern Louisiana shelf under the influence of the Mississippi River is high (approximately 67%) and exceeds the estimate of Suess (1980) for coastal waters, but comparable to previous estimates (short-term deployments) from the area. Of the particulate material exported vertically, 55% is contained in fecal pellets. Export ratios were lowest in summer when the water column was stratified. These results indicate that the system alternates between favoring production export under the influence of increased nutrient availability in spring and *in situ* recycling and retention during summer.

The contribution of fecal pellet carbon to the particulate organic flux ranged from near 0 to 100%, but averaged 55%. The phytoplankton carbon flux contribution to particulate organic carbon flux was substantially lower and ranged from near 0 to 17%, and averaged 4%. The relative differences between FPC and P_{cell} fluxes were most pronounced in spring, somewhat lower in summer, and lowest in fall. The same seasonal trends were seen in phytoplankton carbon flux and in fecal pellet carbon flux. Comparative data for these fluxes were available only for 1991, when sediment trap deployments began in mid-April (Q. Dortch pers. comm., Chapter 3), and showed that the flux of carbon in fecal pellets was an order of magnitude greater than phytoplankton cell carbon flux for both top and bottom traps in 1991. These fluxes may occur directly as phytoplankton cells, or indirectly as fecal pellets and aggregates (which may include phytoplankton cells as well as fecal pellets). A massive flux of ungrazed phytoplankton cells from high surface production earlier in the spring cannot be ruled out, but peak river flow occurred later in spring 1991 than usual (early May cf. March - April, Fig. 1.2). The long-term trend is for net surface water production to lag one month behind peak river flow and for bottom water oxygen deficiency to lag two months behind peak river flow (Justic' et al. 1993). Overall, the flux of fecal pellet carbon to the seabed far exceeded that of phytoplankton cells.

Estimated oxygen depletion rates for the particulate, fecal pellet and phytoplankton carbon fluxed at 15 m were high in spring 1991. The oxygen depletion rates for fecal pellets far exceeded the potential rate due to phytoplankton carbon. Fecal pellet carbon fluxes in spring 1991 alone were sufficient to create low dissolved oxygen bottom waters or hypoxia which was sustained and maintained through the summer in a stratified water column. The fecal pellet carbon flux into the bottom trap was low in spring in 1992 and phytoplankton carbon flux was not calculated. However, POC flux (which includes both fecal pellet and phytoplankton carbon) was sufficient to deplete the bottom water oxygen. POC and FPC fluxes were lower in summer, but were

sufficient to deplete oxygen, especially if the oxygen concentration was already low. The data and calculations support the initial hypothesis that development of summer hypoxia is associated with the decomposition of organic matter accumulated in spring, primarily by the sedimentation of a surface water organic material via fecal pellets, rather than as intact phytoplankton cells.

Mesozooplankton distribution and community composition were studied in the vicinity of the moored sediment traps to identify the organisms which were the potential sources of fecal pellets. The abundance and composition of the mesozooplankton community varied considerably between sample dates. Copepods were the dominant zooplankton, comprising 50 - 60% of the total, followed by oikopleurans, chaetognaths and meroplankton. Copepod numbers were strongly related to zooplankton abundance. There was a negative relationship between mesozooplankton abundance and surface water salinity. This indicated an influence of the Mississippi River discharge on the distribution of copepod communities, which would likely result in high mesozooplankton abundances in spring following the high spring flow. The mesozooplankton samples did not show the same seasonal trends as the fecal pellet fluxes, but zooplankton abundances from the meso- and microzooplankton discrete sampling did. These differences were very likely the result of different sampling frequencies and methods.

The distribution of meso- and microzooplankton and fecal pellets at discrete depths was determined on a monthly and diel scale of variability at station C6B, and on a broad spatial scale across a variety of stations in mid-summer over a continuum of bottom water dissolved oxygen concentrations. Copepod nauplii migrated into the upper water column at night and remained in the lower water column during the day, while the copepods remained concentrated in the lower water column for the full 24-h period. Bottom water oxygen concentrations were not stressful during the 24-h collections and did not disrupt diel vertical migration. Highest densities of total

organisms, copepods and copepod nauplii occurred during March and April when chlorophyll *a* concentrations in the upper water column were highest, and decreased in summer and fall when food resources were reduced. Other possible mechanisms for reduced zooplankton abundances were increased predation, reduced habitat (i.e., oxygen deficient bottom waters), inhibition of copepod egg hatching in oxygen depleted bottom waters and reduced copepod recruitment. The positive correlations of total organisms and copepod nauplii with dissolved oxygen in the lower water column in the monthly collections indicated that higher densities of organisms would occur in the more oxygenated waters and/or organisms would avoid bottom waters low in dissolved oxygen. Within the stations sampled across the hypoxic zone in mid-summer, there were no significant differences in abundances between stations varying in bottom water dissolved oxygen concentrations. Although copepods were present in the bottom waters at all stations and at all depths for the spatial survey, copepod nauplii were not present in the lower water column at stations that were severely hypoxic.

The positive correlation of number of fecal pellets with the abundances of total organisms, copepods and copepod nauplii indicated that these organisms are the likely source. Similarities were observed between the seasonal pattern of meso- and microzooplankton and the flux of fecal pellets into the moored sediment traps at station C6B. High fecal pellet flux of smaller > 20 μm fecal pellets into the top trap in fall paralleled the high concentration of fecal pellets (present in > 20 μm fraction) in the upper water column in September, and were strongly correlated with abundance of microzooplankton. Similarly, higher fluxes of fecal pellets occurred into the sediment traps in spring, when meso- and microzooplankton abundances were higher.

This long term study elucidated an important feature of the system, that alternates between a system favoring production export in spring when the water column is mixed to *in situ* recycling system in summer when it is stratified. Sediment

trap flux data as well as meso- and microzooplankton discrete depth data illustrated that variation in the export ratios were closely related to biological and physical processes.

APPENDIX A

RESUSPENSION POTENTIAL OF SEDIMENTS AND FECAL PELLETS

Sediment Resuspension Potential

I examined the potential of bottom currents to resuspend sediments by determining the critical bed shear stress from Shield's entrainment function θ_c, which is related to the threshold condition for sediment motion, critical shear stress, τ_c (dynes cm^{-2}) by:

τ_c (dynes cm^{-2})= θ_c (ρ_s - ρ) g D Equation A.1

where

θ_c, Shield's entrainment function, was obtained from the empirical Shield's curve (Miller et al. 1977)

ρ_s is the density of inorganic sediment (quartz) particle (2.65 g cm^{-3}, Dyer 1986)

ρ is the density of water (1 g cm^{-3})

g is the gravity (980 cm s^{-2})

D is the diameter of average sediment grain in cm (where sediment grain size $\phi = -\log_2 D$).

U_{*c}, the critical shear velocity expressed as speed required for the movement of a sediment particle (cm s^{-1}),was estimated by:

U_{*c} (cm s^{-1}) = $\sqrt{(\tau_c/\rho)}$ Equation A.2

The critical shear velocity for sediment grain size 6 ϕ to 1 ϕ ranged between 1.23 and 1.58 cm s^{-1}, and the bed critical shear stress, τ_c, ranged between 1.29 and 2.51 dynes cm^{-2} (Table A.1). Sediment particles can be resuspended when the bed shear

stress, $\tau_o > \tau_c$. The bed shear stress was calculated using the relationship between current speed U_{1m} 1 m above the bottom and the drag coefficient C_D (which was assumed to be $3.1*10^{-3}$, following Sternberg (1972) and Wright et al. (1990)). The relationship is expressed as:

$$\tau_o = \rho C_D U^2_{1m} \qquad \text{Equation A.3}$$

which can be rewritten as

$$\tau_c/\rho = \sqrt{U*_c^2} = \sqrt{U*^2/C_D} \qquad \text{Equation A.4}$$

$$\text{or} \quad U* = U*_c/\sqrt{C_D} \qquad \text{Equation A.5}$$

The critical shear velocity $U*_c$ estimated from Equation A.2 and substituted in equation A.5 gave a critical velocity (U*) within the range of 22 to 28 cm s^{-1} and an average of 24.5 cm s^{-1} for sediment grain sizes ranging from 1 ϕ to 6 ϕ (Table A.1). Current meter data (Endeco model 174) from 1 m above the bed were obtained for the period May 10 to August 24, 1992 (Figure A.1, W. J. Wiseman, Jr. unpubl. data). Measured currents ranged from 3 to 20 cm s^{-1}, and in only 3 short intervals, were currents > 24.5 cm s^{-1} and thus capable of resuspending silt particles. The critical velocity (U*) was normally higher than the velocity U_{1m} measured at 1 m above the bottom; therefore, the chances of resuspension of sediment particles during the period of recorded currents were not very likely. Spring and fall current meter data were not available; however, frequent frontal passages during spring and fall along with sustained high winds and increased likely resuspend and transport sediments (Adams et al. 1987).

Resuspension Potential of Fecal Pellets

Fecal pellets ranged in length from 118.9 to 468 mm in the > 63 µm size fraction and from 30.4 to 82.4 µm in the > 20 µm size fraction (Table A.2). The width

Table A.1. Characteristics of sediments: grain size, diameter, critical stress, critical velocity and calculated speed (U*) at 1 m above the seabed.

Grain size phi	Diameter cm	Shield's Criteria†	Critical Stress dynes/cm^2	Critical Velocity U*c cm/s	Velocity U* cm/s
1	0.0500	0.03	2.51	1.58	28.38
2	0.0250	0.05	1.82	1.35	24.25
3	0.0125	0.08	1.62	1.27	22.85
4	0.0063	0.15	1.52	1.23	22.11
5	0.0031	0.35	1.50	1.33	23.89
6	0.0016	0.80	1.29	1.42	25.50
				Mean =	24.50

† values were obtained from Shield's curve (Miller et al. 1977).

Table A.2. Resuspension potential of fecal pellets calculated from length, width, nominal diameter, and density of fecal pellets (1.22 g cm^{-3}, Komar et al. 1981), critical stress, critical velocity, and calculated velocity (U*) at 1 m above the seabed.

Fecal Pellet Length µm	Fecal Pellet Width µm	Nominal Diameter D µm	Nominal Diameter D cm	Shield's Criteria†	Critical Stress dynes/cm^2	Critical Velocity U*c cm/s	Velocity U* cm/s
17.11	14.38	17.44	0.0017	0.420	0.15	0.39	7.09
30.42	17.35	23.95	0.0024	0.360	0.18	0.42	7.69
31.94	17.56	24.54	0.0025	0.350	0.18	0.42	7.68
32.54	17.91	25.02	0.0025	0.350	0.18	0.42	7.75
32.99	18.29	25.49	0.0025	0.350	0.18	0.43	7.82
33.24	18.81	26.03	0.0026	0.330	0.18	0.42	7.68
35.51	19.01	26.80	0.0027	0.330	0.18	0.43	7.79
35.56	20.43	28.13	0.0028	0.325	0.19	0.43	7.92
38.97	20.59	29.15	0.0029	0.320	0.19	0.44	8.00
39.59	21.19	29.88	0.0030	0.300	0.18	0.43	7.84
40.29	29.74	37.67	0.0038	0.280	0.22	0.47	8.51
73.32	31.21	47.49	0.0047	0.180	0.18	0.42	7.66
75.25	31.55	48.25	0.0048	0.180	0.18	0.42	7.72
76.47	32.49	49.47	0.0049	0.150	0.15	0.39	7.13
77.18	33.14	50.28	0.0050	0.150	0.16	0.39	7.19
77.86	33.26	50.55	0.0051	0.150	0.16	0.40	7.21
78.09	33.71	51.06	0.0051	0.150	0.16	0.40	7.25
78.88	34.39	51.92	0.0052	0.150	0.16	0.40	7.31
78.88	36.77	54.29	0.0054	0.150	0.17	0.41	7.47
81.95	38.14	56.34	0.0056	0.150	0.17	0.42	7.61
82.40	43.57	61.68	0.0062	0.140	0.18	0.42	7.70
114.29	49.72	75.11	0.0075	0.100	0.15	0.39	7.18
118.98	52.79	79.23	0.0079	0.100	0.16	0.40	7.37
119.07	52.98	79.44	0.0079	0.100	0.16	0.40	7.38
125.64	54.88	82.80	0.0083	0.090	0.15	0.39	7.15
127.55	55.03	83.37	0.0083	0.085	0.15	0.38	6.97
131.84	56.70	85.99	0.0086	0.085	0.15	0.39	7.08
133.18	58.61	88.20	0.0088	0.083	0.15	0.39	7.09
135.86	62.90	93.07	0.0093	0.080	0.15	0.39	7.15
145.45	69.16	101.43	0.0101	0.080	0.17	0.41	7.46
285.76	104.88	167.68	0.0168	0.060	0.21	0.46	8.31
305.52	109.44	176.40	0.0176	0.052	0.19	0.43	7.93
332.88	129.20	202.75	0.0203	0.051	0.21	0.46	8.42
337.44	143.64	218.58	0.0219	0.050	0.22	0.47	8.66
346.56	145.92	222.86	0.0223	0.050	0.23	0.48	8.74
355.68	155.04	234.07	0.0234	0.040	0.19	0.44	8.01
383.04	182.40	267.38	0.0267	0.037	0.20	0.45	8.24
396.72	246.24	330.44	0.0330	0.030	0.20	0.45	8.25
468.16	269.04	370.43	0.0370	0.025	0.19	0.44	7.97
						Mean =	7.26

† values were obtained from Shield's curve (Miller et al. 1977).

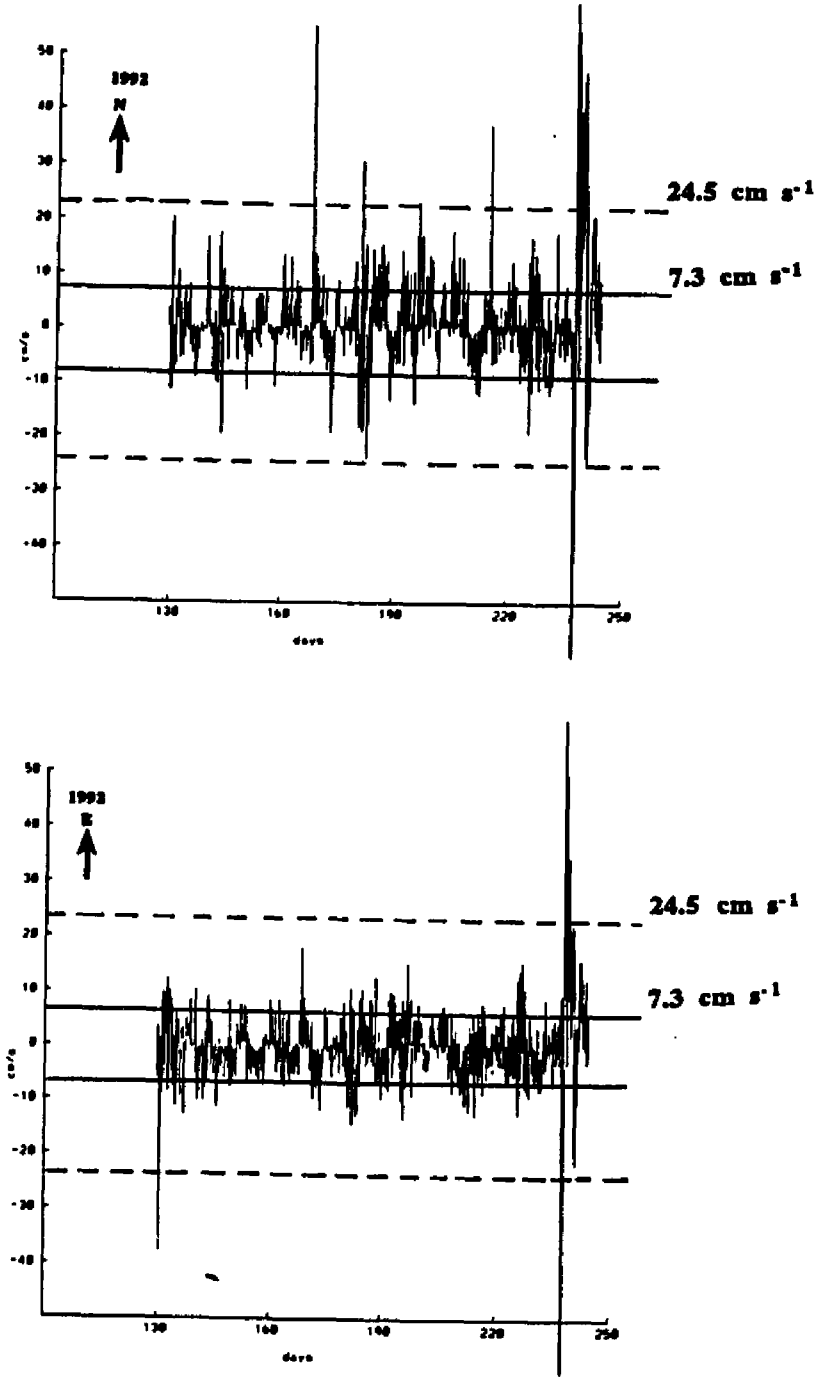


Figure A.1. Time series bottom current data (cm s^{-1}) at 1 m above the seabed from the moored current meter at station C6B during May 10 to August 24, 1992; U vector (upper panel) and V vector (lower panel). Horizontal lines indicate the mean critical velocity that will resuspend silt particles and fecal pellets, 24.50 cm s^{-1} and 7.26 cm s^{-1}, respectively. N.B., end of record marked by passage of Hurricane Andrew.

of fecal pellets ranged from 43.5 to 269 mm in the > 63 mm and from 14.5 to 38.1 mm in the > 20 μm size fraction. Nominal diameters (D), as the diameter of a sphere with the same volume as the pellets, were computed following Taghon et al. (1984) using:

$$D\ (cm) = ((3/2) * d^2 * h)^{(1/3)} \qquad \text{Equation A.6}$$

where d is equal to the width of the pellet and h is equal to the length of the pellet.

I calculated the critical velocity (U*) 1 m above seabed for resuspension of fecal pellets using the nominal diameter. This was estimated from critical shear stress calculated from Equation A.1, where the density of fecal pellets ρ_f was used (ρ_f = 1.22 g cm^{-3}, Komar et al. 1981), and D (cm) was the nominal diameter of the fecal pellet.

The critical velocity (U*) lies in the range of 6.65 to 8.08 cm s^{-1} with an average of 7.26 cm s^{-1} (Table A.2). The critical velocity that will potentially resuspend fecal pellets (7.26 cm s^{-1}) was lower than current velocities measured at 1 m above the bottom for several events in the record (Figure A.1); therefore, fecal pellets are likely to be resuspended and winnowed from the sediment surface during those events.

REFERENCES

ADAMS, C. E. JR., D. J. P. SWIFT, AND J. M. COLEMAN. 1987. Bottom currents and fluviomarine sedimentation on the Mississippi prodelta shelf: February-May 1984. J. Geophy. Res. **92**: 14595-14609.

DYER, K. R. 1986. Coastal and estuarine sediment dynamics. Wiley-Interscience, New York, 342 p.

KOMAR, P. D., A. P. MORSE, L. F. SMALL, AND S. W. FOWLER. 1981. An analysis of sinking rates of natural copepod and euphausiid fecal pellets. Limnol. Oceanogr. **26**: 172-180.

MILLER, M. C., I. N. MCCAVE, AND P. D. KOMAR. 1977. Threshold of sediment motion under unidirectional currents. Sedimentology **24**: 507-527.

STERNBERG, R. W. 1972. Predicting initial motion and bedload transport of sediment particles in the shallow marine environment. p. 61-82. *In*. D. J. Swift, D. B. Duane and O. H. Pilkey [eds.], Shelf sediment transport: process and pattern. Dowden, Hutchinson, and Ross, Stroudsburg, PA.

TAGHON, G. L., A. R. M. NOWELL, AND P. A. JUMARS. 1984. Transport and breakdown of fecal pellets: Biological and sedimentological consequences. Limnol. Oceanogr. **29**: 64-72.

WRIGHT, L. D., W. J. WISEMAN JR., Z. S. YANG, B. D. BORNHOLD, G. H. KELLER, D. P. PRIOR, AND J. N. SUHAYDA. 1990. Processes of marine dispersal and deposition of suspended silts off the modern mouth of the Huanghe (Yellow River). Cont. Shelf Res. **10**: 1-40.

APPENDIX B

SEDIMENT TRAP AND SURFICIAL SEDIMENT DATA USED IN STATISTICAL ANALYSES IN CHAPTER 2 AND CHAPTER 3

Table B.1. 1991 sediment trap data.

Date Retrieved	Season	Top Trap FP 63 µm no. /m^2/d	Top Trap FP 20 µm no. /m^2/d	Top Trap FP Flux no. /m^2/d	Bottom Trap FP 63 µm no. /m^2/d	Bottom Trap FP 20 µm no. /m^2/d	Bottom Trap FP Flux no. /m^2/d	Top Trap FP 63 µm %	Top Trap FP 20 µm %
5/13/91	Spring	2340145.59	1950121.32	4290266.91	1434732.12	5446410.26	6881142.38	54.55	45.45
6/3/91	Spring	1207217.96	560494.05	1767712.01	2647256.53	1957417.69	4604674.22	68.29	31.71
6/25/91	Spring	139927.54	444475.70	584403.24	181082.69	596749.79	777832.48	23.94	76.06
7/1/91	Summer	6601.97	11317.67	17919.64	71678.57	222580.81	294259.38	36.84	63.16
7/9/91	Summer	15561.79	22989.01	38550.81	164106.19	376312.47	540418.67	40.37	59.63
7/23/91	Summer	35569.81	82457.30	118027.11	317703.12	168956.62	486659.74	30.14	69.86
7/29/91	Summer	44327.53	16033.36	60360.90	10374.53	21220.63	31595.16	73.44	26.56
8/13/91	Summer	24898.87	43761.65	68660.52	36971.05	23767.10	60738.15	36.26	63.74
8/19/91	Summer	3300.99	11789.24	15090.22	82053.10	72621.71	154674.80	21.88	78.13
9/12/91	Fall	82996.23	173537.58	256533.82	431957.68	325382.97	757340.64	32.35	67.65
9/17/91	Fall	237671.04	1094418.53	1332089.57	2358602.09	2630226.13	4988828.22	17.84	82.16
10/4/91	Fall	396784.14	906744.96	1303529.10	2093102.91	3131665.42	5224768.32	30.44	69.56
10/17/91	Fall	571106.96	658165.95	1229272.90	3398782.87	5460339.70	8859122.57	46.46	53.54
11/12/91	Fall	170635.62	285553.48	456189.09	268141.68	748707.29	1016848.97	37.40	62.60
12/7/91	Fall	197849.61	487917.26	685766.87	675706.72	1237398.41	1913105.13	28.85	71.15
Mean	Total	**364973.04**	**449985.14**	**814958.18**	**944816.79**	**1494650.47**	**2439467.26**	**38.60**	**61.40**
St Dev		631016.24	540501.95	1171518.19	1135816.87	1876653.30	3012470.17	16.08	16.08
Mean	Spring	**1229097.03**	**985030.36**	**2214127.39**	**1421023.78**	**2666859.25**	**4087883.03**	**48.93**	**51.07**
St Dev		1100272.19	837803.97	1938076.15	1233144.06	2501456.01	3734600.07	22.70	22.70
Mean	Summer	**21710.16**	**31391.37**	**53101.53**	**113814.43**	**147576.56**	**261390.98**	**39.82**	**60.18**
St Dev		16240.45	27764.79	44005.24	112684.33	138069.33	250753.66	17.71	17.71
Mean	Fall	**276173.93**	**601056.29**	**877230.23**	**1537715.66**	**2255619.99**	**3793335.64**	**32.22**	**67.78**
St Dev		177541.79	356434.59	533976.39	1266764.30	1908475.30	3175239.59	9.50	9.50

FP = fecal pellet flux
FPC = fecal pellet carbon
Pcell = Phytoplankton carbon flux
TPM = total particulate material
POC = particulate organic carbon
PON = particulate organic nitrogen
TOC= total organic carbon

(table con'd)

Date Retrieved	Bottom Trap FP 63 µm %	Bottom Trap FP 20 µm %	Top Trap FPC 63 µm mg C/m^2/d	Top Trap FPC 20 µm mg C/m^2/d	Bottom Trap FPC 63 µm mg C/m^2/d	Bottom Trap FPC 20 µm mg C/m^2/d	Top Trap FPC 63 µm %	Top Trap FPC 20 µm %	Bottom Trap FPC 63 µm %
5/13/91	20.85	79.15	4713.13	105.17	522.14	26.03	97.82	2.18	95.25
6/3/91	57.49	42.51	1483.31	21.02	851.74	64.09	98.60	1.40	93.00
6/25/91	23.28	76.72	153.85	22.99	14.60	14.04	87.00	13.00	50.99
7/1/91	24.36	75.64	1.44	0.41	227.03	5.66	77.63	22.37	97.57
7/9/91	30.37	69.63	26.66	1.09	11.31	17.07	96.06	3.94	39.84
7/23/91	65.28	34.72	219.08	2.40	25.35	4.03	98.91	1.09	86.27
7/29/91	32.84	67.16	393.85	0.74	10.13	0.27	99.81	0.19	97.42
8/13/91	60.87	39.13	208.27	1.95	27.71	0.37	99.07	0.93	98.68
8/19/91	53.05	46.95	125.59	0.44	90.77	3.56	99.65	0.35	96.23
9/12/91	57.04	42.96	377.32	2.49	79.51	7.04	99.34	0.66	91.87
9/17/91	47.28	52.72	7.04	12.01	430.34	55.06	36.96	63.04	88.66
10/4/91	40.06	59.94	98.76	30.64	336.47	111.19	76.32	23.68	75.16
10/17/91	38.36	61.64	757.20	20.70	388.32	178.96	97.34	2.66	68.45
11/12/91	26.37	73.63	409.60	12.85	50.89	25.47	96.96	3.04	66.64
12/7/91	35.32	64.68	698.62	7.91	293.36	57.50	98.88	1.12	83.61
Mean Total	**40.85**	**59.15**	**644.91**	**16.19**	**223.98**	**38.02**	**90.69**	**9.31**	**81.98**
St Dev	14.95	14.95	1190.53	26.54	246.61	50.05	16.79	16.79	18.18
Mean Spring	**33.87**	**66.13**	**2116.76**	**49.73**	**462.83**	**34.72**	**94.47**	**5.53**	**79.75**
St Dev	20.49	20.49	2344.72	48.03	421.71	26.13	6.48	6.48	24.93
Mean Summer	**44.46**	**55.54**	**162.48**	**1.17**	**65.38**	**5.16**	**95.19**	**4.81**	**86.00**
St Dev	17.40	17.40	144.62	0.83	84.59	6.21	8.71	8.71	23.07
Mean Fall	**40.74**	**59.26**	**391.43**	**14.43**	**263.15**	**72.54**	**84.30**	**15.70**	**79.07**
St Dev	10.49	10.49	304.00	9.96	160.43	63.02	24.80	24.80	10.57

(table con'd)

Date Retrieved	Bottom Trap FPC 20 µm %	Top Trap FPC mg C/m^2/d	Bottom Trap FPC mg C/m^2/d	Top Trap TPM mg /m^2/d	Bottom Trap TPM mg /m^2/d	Top Trap POC mg C/m^2/d	Bottom Trap POC mg C/m^2/d	Top Trap PON mg/m^2/d	Bottom Trap PON mg/m^2/d
5/13/91	4.75	4818.30	548.17	96809.59	68428.36	7018.27	998.69	1032.78	96.72
6/3/91	7.00	1504.33	915.83	137967.77	96793.01	2737.27	927.37	345.41	72.97
6/25/91	49.01	176.84	28.64	14944.47	40846.49	1420.11	452.07	218.15	54.43
7/1/91	2.43	1.85	232.69	6625.55	17495.23	586.31	240.99	92.15	34.87
7/9/91	60.16	27.76	28.38	3607.51	6879.02	123.43	172.64	22.09	26.24
7/23/91	13.73	221.48	29.38	8022.23	7589.50	352.94	316.12	54.05	46.44
7/29/91	2.58	394.59	10.40	15184.54	7710.16	735.27	164.97	106.06	22.32
8/13/91	1.32	210.22	28.08	16297.44	3300.99	924.63	67.87	116.83	9.04
8/19/91	3.77	126.03	94.34	5140.11	4397.39	225.26	97.69	33.34	13.72
9/12/91	8.13	379.81	86.54	21173.47	11388.40	1263.95	196.55	174.22	24.55
9/17/91	11.34	19.05	485.40	60323.17	44931.14	4690.05	546.40	652.13	59.33
10/4/91	24.84	129.40	447.67	17975.12	148594.33	411.05	1191.19	47.31	121.37
10/17/91	31.55	777.90	567.28	72084.84	289732.31	850.87	1872.08	102.07	169.05
11/12/91	33.36	422.46	76.37	68992.51	149936.47	542.21	721.35	60.48	91.24
12/7/91	16.39	706.53	350.86	20688.70	160077.10	741.28	1330.85	99.49	149.46
Mean Total	**18.02**	**661.10**	**262.00**	**37722.47**	**70539.99**	**1508.19**	**619.79**	**210.44**	**66.12**
St Dev	18.18	1214.91	276.49	40288.38	83606.78	1925.51	539.92	278.90	50.00
Mean Spring	**20.25**	**2166.49**	**497.54**	**83240.61**	**68689.29**	**3725.21**	**792.71**	**532.11**	**74.71**
St Dev	24.93	2390.53	445.75	62624.05	27974.17	2926.92	297.15	438.23	21.20
Mean Summer	**14.00**	**163.65**	**70.54**	**9146.23**	**7895.38**	**491.31**	**176.72**	**70.75**	**25.44**
St Dev	23.07	144.85	84.56	5328.13	5033.14	310.34	91.44	39.68	13.76
Mean Fall	**20.93**	**405.86**	**335.69**	**43539.63**	**134109.96**	**1416.57**	**976.40**	**189.28**	**102.50**
St Dev	10.57	301.93	208.87	26154.62	98352.76	1630.38	605.33	231.03	54.88

(table con'd)

Date Retrieved	Top Trap FPC:POC %	Bottom Trap FPC:POC %	Top Trap Pcell mg C/m^2/d	Bottom Trap Pcell mg C/m^2/d	Top Trap Pcell:POC %	Bottom Trap Pcell:POC %	Top Trap Chlorophyll a mg /m^2/d	Bottom Trap Chlorophyll a mg /m^2/d	Top Trap Phaeopigment mg /m^2/d
5/13/91	68.65	54.89	100.09	36.82	1.43	3.69	1.23	0.24	34.77
6/3/91	54.96	98.76	99.35	11.23	3.63	1.21	0.98	0.59	25.44
6/25/91	12.45	6.34	8.47	4.01	0.60	0.89	0.06	0.02	0.79
7/1/91	0.32	96.55	1.18	1.40	0.20	0.58	0.05	0.03	0.18
7/9/91	22.49	16.44	1.46	0.91	1.18	0.53	0.01	0.03	0.05
7/23/91	62.75	9.29	7.66	2.29	2.17	0.73	0.09	0.03	0.36
7/29/91	53.67	6.30	5.61	4.53	0.76	2.75	0.06	0.04	0.29
8/13/91	22.74	41.36	4.13	9.90	0.45	14.58	0.02	0.00	0.07
8/19/91	55.95	96.56	37.56	6.64	16.67	6.80	0.03	0.00	0.07
9/12/91	30.05	44.03	249.75	20.91	19.76	10.64	0.07	0.00	0.10
9/17/91	0.41	88.84	40.33	11.38	0.86	2.08	0.25	0.18	0.22
10/4/91	31.48	37.58	13.63	8.25	3.32	0.69	0.10	0.20	0.49
10/17/91	91.43	30.30	27.20	71.41	3.20	3.81	0.24	0.69	3.03
11/12/91	77.91	10.59	33.12	16.93	6.11	2.35	0.11	0.48	1.65
12/7/91	95.31	26.36	33.49	86.03	4.52	6.46	0.09	0.16	1.94
Mean Total	**45.37**	**44.28**	**44.20**	**19.51**	**4.32**	**3.85**	**0.23**	**0.18**	**4.63**
St Dev	30.93	34.97	65.09	25.88			0.37	0.23	10.53
Mean Spring	**45.35**	**53.33**	**69.30**	**17.35**	**1.88**	**1.93**	**0.76**	**0.28**	**20.33**
St Dev	29.31	46.23	52.68	17.24			0.61	0.29	17.56
Mean Summer	**36.32**	**44.42**	**9.60**	**4.28**	**3.57**	**4.33**	**0.04**	**0.02**	**0.17**
St Dev	24.73	42.23	13.92	3.49			0.03	0.02	0.13
Mean Fall	**54.43**	**39.62**	**66.25**	**35.82**	**6.29**	**4.34**	**0.14**	**0.28**	**1.24**
St Dev	39.07	26.65	90.34	33.84			0.08	0.25	1.16

(table con'd)

Date Retrieved	Bottom Trap Phaeopigment mg /m^2/d	Top Trap Total pigment mg /m^2/d	Bottom Trap Total pigment mg /m^2/d	Top Trap TOC %	Bottom Trap TOC %	Top Trap C/N	Bottom Trap C/N
5/13/91	6.43	36.00	6.67	5.29	1.35	6.79	12.29
6/3/91	12.40	26.42	12.99	2.05	1.06	8.03	13.03
6/25/91	0.50	0.85	0.52	10.56	1.40	6.55	8.32
7/1/91	0.36	0.23	0.39	9.87	1.53	6.36	6.88
7/9/91	0.22	0.06	0.25	3.69	2.45	5.60	6.60
7/23/91	0.27	0.45	0.30	6.47	4.78	6.54	6.83
7/29/91	0.35	0.35	0.40	4.14	2.36	6.97	7.48
8/13/91	0.28	0.09	0.28	6.85	1.92	7.93	7.51
8/19/91	0.61	0.10	0.61	4.80	2.25	6.83	7.19
9/12/91	0.68	0.18	0.68	5.49	1.23	7.37	8.01
9/17/91	2.34	0.47	2.52	7.53	1.15	7.41	9.20
10/4/91	5.36	0.59	5.56	2.73	0.96	8.80	9.82
10/17/91	8.51	3.27	9.19	1.22	0.63	8.36	11.10
11/12/91	2.21	1.77	2.69	0.80	0.50	9.01	9.72
12/7/91	2.14	2.03	2.30	3.63	0.91	7.52	9.00
Mean Total	**2.84**	**4.86**	**3.02**	**5.01**	**1.63**	**7.34**	**8.87**
St Dev	3.70	10.89	3.89	2.89	1.06	0.96	2.01
Mean Spring	**6.44**	**21.09**	**6.73**	**5.96**	**1.27**	**7.12**	**11.21**
St Dev	5.95	18.17	6.23	4.29	0.18	0.80	2.53
Mean Summer	**0.35**	**0.21**	**0.37**	**5.97**	**2.55**	**6.71**	**7.08**
St Dev	0.14	0.16	0.13	2.29	1.15	0.77	0.37
Mean Fall	**3.54**	**1.38**	**3.82**	**3.57**	**0.90**	**8.08**	**9.47**
St Dev	2.87	1.19	3.07	2.58	0.28	0.74	1.02

Table B.2. 1992 sediment trap data.

Date Retrieved	Season	Top Trap FP 63 µm no. /m^2/d	Top Trap FP 20 µm no. /m^2/d	Top Trap FP Flux no. /m^2/d	Bottom Trap FP 63 µm no. /m^2/d	Bottom Trap FP 20 µm no. /m^2/d	Bottom Trap FP Flux no. /m^2/d	Top Trap FP 63 µm %	Top Trap FP 20 µm %
3/27/92	Spring	65189.77	176827.25	242017.02	nd	nd	nd	26.94	73.06
4/13/92	Spring	46602.16	144466.71	191068.87	58585.58	317826.76	376412.34	24.39	75.61
5/5/92	Spring	31380.81	142332.54	173713.35	995954.82	2474825.84	3470780.66	18.06	81.94
5/26/92	Spring	3772.56	68983.88	72756.44	120721.80	1216272.10	1336993.89	5.19	94.81
6/6/92	Summer	14404.31	48357.31	62761.62	74079.28	386995.67	461074.95	22.95	77.05
6/17/92	Summer	7202.15	61732.74	68934.89	197544.76	893066.92	1090611.68	10.45	89.55
7/6/92	Summer	15487.34	119133.35	134620.69	107220.02	413631.00	520851.01	11.50	88.50
7/20/92	Summer	42037.05	432712.19	474749.24	278091.28	1403390.88	1681482.16	8.85	91.15
7/29/92	Summer	5658.83	30180.45	35839.28	392345.84	2183052.48	2575398.32	15.79	84.21
8/13/92	Summer	808.40	14147.09	14955.49	150363.31	691671.22	842034.53	5.41	94.59
10/6/92	Fall	324883.66	2773760.80	3098644.45	1001280.78	8899149.22	9900430.00	10.48	89.52
10/27/92	Fall	576172.21	4167645.64	4743817.85	1020647.91	21254992.78	22275640.69	12.15	87.85
Mean	**Total**	**94466.60**	**681690.00**	**776156.60**	**399712.31**	**3648624.99**	**4048337.29**	**14.35**	**85.65**
St Dev		175850.14	1340707.17	1516557.31	400828.53	6329056.96	6729885.49	7.30	7.30
Mean	**Spring**	**36736.32**	**133152.60**	**169888.92**	**391754.06**	**1336308.23**	**1728062.29**	**18.64**	**81.36**
St Dev		25962.95	45597.44	71560.39	524174.72	1083497.93	1607672.65	9.72	9.72
Mean	**Summer**	**14266.35**	**117710.52**	**131976.87**	**199940.75**	**995301.36**	**1195242.11**	**12.49**	**87.51**
St Dev		14682.17	158466.62	173148.79	118346.21	691130.83	809477.05	6.15	6.15
Mean	**Fall**	**450527.93**	**3470703.22**	**3921231.15**	**1010964.35**	**15077071.00**	**16088035.35**	**11.32**	**88.68**
St Dev		177687.84	985625.43	1163313.26	13694.63	8736900.76	8750595.39	1.17	1.17

FP = fecal pellet flux
FPC = fecal pellet carbon
TOC= total organic carbon
TPM = total particulate material
POC = particulate organic carbon
PON = particulate organic nitrogen
nd = no data

(table con'd)

Date Retrieved	Bottom Trap FP 63 µm %	Bottom Trap FP 20 µm %	Top Trap FPC 63 µm mg C/m^2/d	Top Trap FPC 20 µm mg C/m^2/d	Bottom Trap FPC 63 µm mg C/m^2/d	Bottom Trap FPC 20 µm mg C/m^2/d	Top Trap FPC 63 µm %	Top Trap FPC 20 µm %	Bottom Trap FPC 63 µm %
3/27/92	nd	nd	69.18	7.80	nd	nd	89.86	10.14	nd
4/13/92	15.56	84.44	24.77	3.88	13.62	11.85	86.46	13.54	53.49
5/5/92	28.70	71.30	2.53	2.57	224.01	74.18	49.64	50.36	75.12
5/26/92	9.03	90.97	1.13	2.74	18.75	191.06	29.20	70.80	8.93
6/6/92	16.07	83.93	41.15	0.46	10.71	12.59	98.89	1.11	45.97
6/17/92	18.11	81.89	0.83	0.65	150.50	8.01	56.06	43.94	94.95
7/6/92	20.59	79.41	5.97	1.33	43.16	9.59	81.84	18.16	81.82
7/20/92	16.54	83.46	10.64	20.42	96.98	31.67	34.25	65.75	75.38
7/29/92	15.23	84.77	43.87	0.27	92.34	41.35	99.38	0.62	69.07
8/13/92	17.86	82.14	2.86	0.19	22.79	13.81	93.86	6.14	62.28
10/6/92	10.11	89.89	397.18	488.34	401.31	201.99	44.85	55.15	66.52
10/27/92	4.58	95.42	910.88	68.32	171.78	463.35	93.02	6.98	27.05
Mean Total	**15.67**	**84.33**	**125.92**	**49.75**	**113.27**	**96.31**	**71.44**	**28.56**	**60.05**
St Dev	6.35	6.35	270.75	139.47	119.68	141.01	26.56	26.56	24.95
Mean Spring	**17.76**	**82.24**	**24.40**	**4.25**	**85.46**	**92.36**	**63.79**	**36.21**	**45.85**
St Dev	10.02	10.02	31.75	2.44	120.02	90.98	29.38	29.38	33.75
Mean Summer	**17.40**	**82.60**	**17.55**	**3.89**	**69.41**	**19.50**	**77.38**	**22.62**	**71.58**
St Dev	1.90	1.90	19.63	8.11	53.23	13.68	26.66	26.66	16.82
Mean Fall	**7.35**	**92.65**	**654.03**	**278.33**	**286.54**	**332.67**	**68.94**	**31.06**	**46.78**
St Dev	3.91	3.91	363.24	297.00	162.31	184.81	34.06	34.06	27.91

(table con'd)

Date Retrieved	Bottom Trap FPC 20 µm %	Top Trap FPC mg C/m^2/d	Bottom Trap FPC mg C/m^2/d	Top Trap TPM mg /m^2/d	Bottom Trap TPM mg /m^2/d	Top Trap POC mg C/m^2/d	Bottom Trap POC mg C/m^2/d	Top Trap PON mg/m^2/d	Bottom Trap PON mg/m^2/d
3/27/92	nd	76.98	nd	2099.43	nd	162.79	nd	19.40	nd
4/13/92	46.51	28.65	25.48	1506.25	15245.57	222.92	274.62	35.80	33.96
5/5/92	24.88	5.10	298.45	2720.10	14190.62	727.39	308.15	132.77	40.89
5/26/92	91.07	3.87	209.83	5241.16	8030.16	877.61	227.20	164.72	33.35
6/6/92	54.03	41.61	23.31	7137.85	16462.06	1672.10	366.61	323.65	60.34
6/17/92	5.05	1.47	158.68	38377.19	12433.71	3742.81	158.77	750.13	22.82
7/6/92	18.18	7.30	52.80	4944.03	6090.69	1626.11	246.17	308.87	39.73
7/20/92	24.62	31.06	128.76	4688.75	26273.16	500.79	945.68	88.79	175.86
7/29/92	30.93	44.14	133.79	4369.88	28168.42	230.50	633.80	37.19	90.75
8/13/92	37.72	3.04	36.63	4759.48	16693.56	152.36	385.11	23.93	52.37
10/6/92	33.48	885.53	603.76	31689.47	111064.05	886.87	1095.04	115.41	120.49
10/27/92	72.95	979.19	635.32	40528.03	83642.96	1227.89	653.57	163.60	77.06
Mean Total	**39.95**	**175.66**	**209.71**	**12338.47**	**30754.09**	**1002.51**	**481.34**	**194.99**	**67.97**
St Dev	24.95	354.73	219.65	14995.06	34133.28	1017.36	310.52	209.90	46.07
Mean Spring	**54.15**	**28.65**	**177.92**	**2891.73**	**12488.78**	**497.68**	**269.99**	**111.10**	**36.07**
St Dev	33.75	34.18	139.25	1642.82	3897.14	358.12	40.67	67.14	4.19
Mean Summer	**28.42**	**21.44**	**88.99**	**10712.86**	**17686.93**	**1320.78**	**456.02**	**255.43**	**73.65**
St Dev	16.82	19.76	57.99	13589.27	8344.35	1364.49	288.72	276.13	54.96
Mean Fall	**53.22**	**932.36**	**619.54**	**36108.75**	**97353.51**	**1057.38**	**874.30**	**139.51**	**98.78**
St Dev	27.91	66.23	22.32	6249.81	19389.64	241.13	312.17	34.08	30.71

(table con'd)

Date Retrieved	Top Trap FPC:POC %	Bottom Trap FPC:POC %	Top Trap Chlorophyll a mg /m^2/d	Bottom Trap Chlorophyll a mg /m^2/d	Top Trap Phaeopigment mg /m^2/d	Bottom Trap Phaeopigment mg /m^2/d	Top Trap Total pigment mg /m^2/d	Bottom Trap Total pigment mg /m^2/d
3/27/92	47.29	nd	0.20	nd	0.20	nd	0.39	nd
4/13/92	12.85	9.28	0.04	1.02	0.16	1.13	0.20	2.15
5/5/92	0.70	96.85	0.10	0.16	0.33	0.69	0.44	0.84
5/26/92	0.44	92.35	0.03	0.05	0.22	0.43	0.24	0.48
6/6/92	2.49	6.36	0.02	0.17	0.38	1.07	0.41	1.23
6/17/92	0.04	99.94	0.15	0.08	0.76	0.30	0.90	0.37
7/6/92	0.45	21.45	0.17	0.00	0.78	2.32	0.95	2.26
7/20/92	6.20	13.62	0.03	0.00	0.16	3.37	0.18	3.02
7/29/92	19.15	21.11	0.02	0.00	0.10	6.15	0.12	5.51
8/13/92	2.00	9.51	0.01	0.00	0.04	2.80	0.05	2.39
10/6/92	99.85	55.14	0.07	0.23	1.83	2.28	1.91	2.52
10/27/92	79.75	97.21	0.10	0.31	2.88	1.66	2.98	1.97
Mean Total	**22.60**	**47.53**	**0.08**	**0.18**	**0.65**	**2.02**	**0.73**	**2.07**
St Dev	34.40	41.04	0.06	0.30	0.86	1.70	0.88	1.44
Mean Spring	**15.32**	**66.16**	**0.09**	**0.41**	**0.23**	**0.75**	**0.32**	**1.16**
St Dev	22.09	49.31	0.08	0.53	0.08	0.36	0.11	0.88
Mean Summer	**5.05**	**28.66**	**0.06**	**0.04**	**0.37**	**2.67**	**0.43**	**2.47**
St Dev	7.24	35.44	0.07	0.07	0.33	2.05	0.40	1.76
Mean Fall	**89.80**	**76.17**	**0.09**	**0.27**	**2.36**	**1.97**	**2.44**	**2.24**
St Dev	14.21	29.75	0.02	0.06	0.74	0.44	0.76	0.39

(table con'd)

Date Retrieved	Top Trap TOC %	Bottom Trap TOC %	Top Trap C/N	Bottom Trap C/N
3/27/92	7.90	nd	8.63	nd
4/13/92	14.64	1.76	6.23	8.08
5/5/92	29.08	2.14	5.48	7.56
5/26/92	15.36	2.51	5.34	6.89
6/6/92	26.94	2.11	5.17	6.16
6/17/92	13.75	1.68	5.00	6.93
7/6/92	34.23	4.92	5.26	6.24
7/20/92	12.71	3.60	5.71	6.24
7/29/92	6.61	2.89	6.38	7.05
8/13/92	5.75	7.39	6.45	7.44
10/6/92	2.84	1.13	7.70	9.05
10/27/92	6.70	0.87	7.57	8.60
Mean Total	**15.33**	**2.82**	**6.03**	**7.29**
St Dev	10.18	1.90	1.90	1.90
Mean Spring	**19.69**	**2.14**	**5.68**	**7.51**
St Dev	8.88	0.38	0.38	0.38
Mean Summer	**16.66**	**3.76**	**5.66**	**6.68**
St Dev	11.48	2.11	2.11	2.11
Mean Fall	**4.77**	**1.00**	**7.64**	**8.82**
St Dev	2.73	0.18	0.18	0.18

Table B.3. 1991 surficial sediment data.

Date Collected	Season	FP no./m^2	FP 63 µm no./m^2	FP 20 µm no./m^2	FP 63 µm %	FP 20 µm %	FPC mg C/m^2	FPC 63 µm mg C/m^2	FPC 20 µm mg C/m^2
02.2.91	Spring	14807093.40	5070048.31	9737045.09	34.24	65.76	1326.37	1072.14	254.23
02.28.91	Spring	32646618.36	5862318.84	26784299.52	17.96	82.04	2364.59	1692.21	672.38
03.28.91	Spring	39098727.86	12391304.35	26707423.51	31.69	68.31	3388.53	2821.80	566.73
04.17.91	Spring	28380917.87	11642512.08	16738405.80	41.02	58.98	3727.78	3305.33	422.45
05.17.91	Spring	46529951.69	11621256.04	34908695.65	24.98	75.02	3786.09	2500.15	1285.95
06.17.91	Summer	60679549.11	13855072.46	46824476.65	22.83	77.17	5457.62	3194.34	2263.28
07.26.91	Summer	61025352.66	33507246.38	27518106.28	54.91	45.09	7915.09	6888.20	1026.88
08.13.91	Summer	85255748.79	23594202.90	61661545.89	27.67	72.33	10114.60	7999.41	2115.19
09.17.91	Fall	43852560.39	16451690.82	27400869.57	37.52	62.48	5529.23	4812.63	716.60
10.17.91	Fall	49648502.42	10106280.19	39542222.22	20.36	79.64	3059.90	2332.92	726.97
12.11.91	Fall	78364734.30	13893719.81	64471014.49	17.73	82.27	5958.44	4978.73	979.71
Mean	Total	**49117250.62**	**14363241.11**	**34754009.52**	**30.08**	**69.92**	**4784.38**	**3781.62**	**1002.76**
St Dev		20114274.01	7699492.97	16406385.28	10.83	10.83	2439.22	2064.36	622.46
Mean	Spring	**32292661.84**	**9317487.92**	**22975173.91**	**29.98**	**70.02**	**2918.67**	**2278.32**	**640.35**
St Dev		11939379.03	3540493.22	9810624.31	8.84	8.84	1057.15	894.11	393.64
Mean	Summer	**68986883.52**	**23652173.91**	**45334709.61**	**35.14**	**64.86**	**7829.10**	**6027.32**	**1801.79**
St Dev		14090311.49	9826215.21	17120402.20	17.29	17.29	2329.68	2515.55	675.16
Mean	Fall	**57288599.03**	**13483896.94**	**43804702.09**	**25.20**	**74.80**	**4849.19**	**4041.43**	**807.76**
St Dev		18481094.24	3192495.12	18899086.28	10.75	10.75	1564.36	1481.94	149.00

FP = fecal pellet
FPC = fecal pellet carbon
TOC = total organic carbon

(table con'd)

Date Collected	FPC 63 µm %	FPC 20 µm %	Chlorophyll a µg/g dry wt	Phaeopigment µg/g dry wt	Total pigment µg/g dry wt	TOC %	Sand %	Silt %	Clay %
02.02.91	80.83	19.17	0.95	31.88	32.83	1.39	28.76	68.94	2.30
02.28.91	71.56	28.44	12.04	49.78	61.82	0.96	nd	nd	nd
03.28.91	83.27	16.73	7.23	48.29	55.52	1.10	26.46	72.75	0.79
04.17.91	88.67	11.33	8.37	102.07	110.44	0.37	7.26	84.93	7.82
05.17.91	66.04	33.96	12.36	73.37	85.73	0.98	6.88	86.13	6.99
06.17.91	58.53	41.47	7.51	87.92	95.43	1.44	7.85	85.05	7.10
07.26.91	87.03	12.97	1.34	25.00	26.34	0.44	32.20	65.82	1.97
08.13.91	79.09	20.91	nd	nd	nd	nd	nd	nd	nd
09.17.91	87.04	12.96	2.70	62.84	65.54	0.93	11.14	87.08	1.78
10.17.91	76.24	23.76	0.84	21.51	22.35	0.61	12.57	85.12	2.32
12.11.91	83.56	16.44	2.62	39.88	42.50	0.92	19.26	78.23	2.51
Mean Total	**78.35**	**21.65**	**5.60**	**54.25**	**59.85**	**0.91**	**16.93**	**79.34**	**3.73**
St Dev	9.10	9.10	4.25	25.59	28.48	0.34	9.42	7.74	2.58
Mean Spring	**78.07**	**21.93**	**8.19**	**61.08**	**69.27**	**0.96**	**17.34**	**78.19**	**4.48**
St Dev	9.14	9.14	4.63	27.27	29.74	0.37	11.90	8.63	3.46
Mean Summer	**74.88**	**25.12**	**4.43**	**56.46**	**60.89**	**0.94**	**20.03**	**75.44**	**4.54**
St Dev	14.71	14.71	4.36	44.49	48.85	0.71	17.22	13.60	3.63
Mean Fall	**82.28**	**17.72**	**2.05**	**41.41**	**43.46**	**0.82**	**14.32**	**83.48**	**2.20**
St Dev	5.51	5.51	1.05	20.71	21.61	0.18	4.33	4.65	0.38

Table B.4. 1992 surficial sediment data.

Date Collected	Season	FP no./m^2	FP 63 µm no./m^2	FP 20 µm no./m^2	FP 63 µm %	FP 20 µm %	FPC mg C/m^2	FPC 63 µm mg C/m^2	FPC 20 µm mg C/m^2
02.28.92	Spring	57832608.70	36289855.07	21542753.62	62.75	37.25	12281.21	11653.60	627.61
03.04.92	Spring	61426086.96	38782608.70	22643478.26	63.14	36.86	8977.55	8501.78	475.77
03.27.92	Spring	57396014.49	33101449.28	24294565.22	57.67	42.33	25578.11	24643.09	935.02
04.13.92	Spring	64612318.84	26086956.52	38525362.32	40.37	59.63	8765.74	7822.04	943.70
05.26.92	Spring	98242753.62	45565217.39	52677536.23	46.38	53.62	12827.00	11020.89	1806.11
06.17.92	Summer	37072463.77	18202898.55	18869565.22	49.10	50.90	21162.21	20564.16	598.04
07.25.92	Summer	47499275.36	10231884.06	37267391.30	21.54	78.46	3308.39	2280.20	1028.19
08.12.92	Summer	16749275.36	3855072.46	12894202.90	23.02	76.98	3012.47	2752.84	259.62
09.18.92	Fall	7384782.61	623188.41	6761594.20	8.44	91.56	208.53	62.51	146.02
10.27.92	Fall	29352898.55	8753623.19	20599275.36	29.82	70.18	2382.71	1915.60	467.11
Mean	**Total**	**47756847.83**	**22149275.36**	**25607572.46**	**40.22**	**59.78**	**9850.39**	**9121.67**	**728.72**
St Dev		26370263.41	15970380.37	13539738.41	18.91	18.91	8368.67	8200.95	478.25
Mean	**Spring**	**67901956.52**	**35965217.39**	**31936739.13**	**54.06**	**45.94**	**13685.92**	**12728.28**	**957.64**
St Dev		17212561.95	7176076.38	13475840.18	10.21	10.21	6901.30	6855.06	515.20
Mean	**Summer**	**33773671.50**	**10763285.02**	**23010386.47**	**31.22**	**68.78**	**9161.02**	**8532.40**	**628.62**
St Dev		15638163.19	7188659.03	12703262.52	15.50	15.50	10394.38	10422.49	385.19
Mean	**Fall**	**18368840.58**	**4688405.80**	**13680434.78**	**19.13**	**80.87**	**1295.62**	**989.05**	**306.57**
St Dev		15533803.75	5749085.57	9784718.18	15.12	15.12	1537.38	1310.33	227.04

FP = fecal pellet
FPC = fecal pellet carbon
TOC = total organic carbon

(table con'd)

Date Collected	FPC 63 µm %	FPC 20 µm %	Chlorophyll a µg/g dry wt	Phaeopigment µg/g dry wt	Total pigment µg/g dry wt	TOC %	Sand %	Silt %	Clay %
02.28.92	94.89	5.11	0.55	26.14	26.69	0.89	19.46	78.80	1.74
03.04.92	94.70	5.30	1.78	20.60	22.38	1.00	8.08	88.85	3.07
03.27.92	96.34	3.66	15.87	35.91	51.78	0.62	7.61	90.00	2.39
04.13.92	89.23	10.77	3.21	26.77	29.98	0.93	15.40	82.45	2.15
05.26.92	85.92	14.08	4.73	24.95	29.68	0.94	24.04	74.16	1.80
06.17.92	97.17	2.83	18.59	83.23	101.82	0.31	17.43	80.39	2.18
07.25.92	68.92	31.08	3.56	45.60	49.16	nd	nd	nd	nd
08.12.92	91.38	8.62	2.27	27.90	30.17	1.44	4.40	92.45	3.15
09.18.92	29.98	70.02	3.30	28.99	32.29	0.43	5.39	91.30	3.31
10.27.92	80.40	19.60	6.57	40.36	46.93	1.14	4.10	92.79	3.11
Mean Total	**82.89**	**17.11**	**6.04**	**36.05**	**42.09**	**0.86**	**11.77**	**85.69**	**2.54**
St Dev	20.52	20.52	6.15	18.25	23.33	0.35	7.41	6.85	0.62
Mean Spring	**92.22**	**7.78**	**5.23**	**26.87**	**32.10**	**0.88**	**14.92**	**82.85**	**2.23**
St Dev	4.44	4.44	6.15	5.60	11.42	0.15	7.15	6.69	0.54
Mean Summer	**85.83**	**14.17**	**8.14**	**52.24**	**60.38**	**0.88**	**10.92**	**86.42**	**2.67**
St Dev	14.92	14.92	9.07	28.26	37.12	0.80	9.21	8.53	0.69
Mean Fall	**55.19**	**44.81**	**4.94**	**34.68**	**39.61**	**0.79**	**4.75**	**92.05**	**3.21**
St Dev	35.65	35.65	2.31	8.04	10.35	0.50	0.91	1.05	0.14

VITA

Naureen Aziz Qureshi was born August 7, 1954 in Lahore, Pakistan. She graduated from the University of Karachi, Pakistan in 1974 with a B. S. degree in Biology. She received M. S. degree from the Zoology Department, University of Karachi, Pakistan in 1977 with a specialization in Marine Zoology, with first class first position (gold medalist). She worked in the Zoological Survey of Pakistan for two years. In 1981, she received a two year Junior Research Fellow scholarship from the University Grants Commission, for a M. Phil. in Marine Biology at the Center of Excellence in Marine Biology, University of Karachi, during which she worked on Indian Ocean sergestid shrimps of the family Penaeidae. She started working at the Center temporarily in 1983 as a Research Officer, after her completion of M. Phil degree. She was nominated by Ministry of Education, Pakistan and was awarded a USAID Thomas Jefferson scholarship for Ph.D. studies and entered Louisiana State University in fall 1989. She will return to join her job at the Center of Excellence in Marine Biology, University of Karachi, Pakistan.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Naureen Aziz Qureshi

Major Field: Oceanography and Coastal Sciences

Title of Dissertation: The Role of Fecal Pellets in the Flux of Carbon to the Sea Floor on a River-Influenced Continental Shelf Subject to Hypoxia

Approved:

Nancy N. Rabalais
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

12/02/94