INFLUENCE OF NATURAL AND ANTHROPOGENIC DISTURBANCE ON THE SOFT BOTTOM MACROBENTHIC COMMUNITY OF THE CAMPECHE BANK, MEXICO

by

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ABSTRACT

INFLUENCE OF NATURAL AND ANTHROPOGENIC DISTURBANCE ON THE SOFT BOTTOM MACROBENTHIC COMMUNITY OF THE CAMPECHE BANK, MEXICO

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The structure of macrobenthic communities was investigated in carbonate and transitional carbonate-terrigenous sediments of the Southern Gulf of Mexico (Campeche Bank). The aim was to assess the influence of natural disturbance represented by winter storms and river runoff and the putative influence of oil-related activities using a regional approach.

At a scale of >100 km community composition of benthic macroinfauna was characterised as distinct assemblages within the carbonate and transitional sedimentary provinces controlled by natural disturbance. The carbonate assemblage was numerous and diverse influenced by a heterogeneous substratum. Winter storms had a severe impact with mortality probably resulting from abrasion and passive transport causing low values of number of taxa, abundance, biomass and diversity measurements. Conversely, on the transitional shelf a sequence of disturbance from river runoff and winter storms resulted in a general impoverished community due to fine sedimentation and sediment instability. Immediately after the rainy season, values of biological measures were low, but the severity of disturbance was contingent with depth.

At a scale of 10s km within the transitional shelf, the combined effect from natural and anthropogenic disturbance caused extremely low values of biological measures within the so called oil exclusion zone. Despite the lack of adequate controls the effects of oil related activities were identified as severe reductions in macroinfauna densities and biomass resulting in a very simple community. Large spatial variability at this scale masks the temporal variation observed in other areas of the Campeche Bank and the relationship between biological measures and indicators of oil activities (Barium, Nickel and oil-hydrocarbons). Finally the increased variability resulting from the influence of oil activities interrupts the natural gradient of macroinfauna patterns across the shelf.

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Author's declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Signed ....

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CHAPTER 1

INTRODUCTION

Disturbance ecology

A disturbance can be defined as "any relative discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White & Picket 1985). Disturbance operates over a broad scale of both time and space and can be categorised by its intensity, frequency, area influenced and its effect on existing resources (Petraitis *et al.* 1989, Huston 1994, Begon *et al.* 1996). Disturbance can occur regularly or stochastically, with regular disturbances reducing the ability of certain species to remain continuously in an area (Wolda 1987) and random events often causing a severe or catastrophic decline in species populations (Middleton 1999).

Disturbance is seen as a continuum of environmental and biological processes where at the extremes, a condition of non-equilibrium (maximum disturbance) and equilibrium (minimum disturbance) in biological diversity may exist (White & Picket 1985, Giller & Gee 1987). The development of the pervasive intermediate disturbance (Grime 1973, Horn 1975, Connell 1978 and Wilkinson 1999 for a historic account) and dynamic equilibrium hypotheses (Huston 1979) demonstrate that disturbance is considered a key aspect of community ecology, particularly as a mechanism determining species diversity. The intermediate disturbance hypothesis predicts that at very high and very low frequencies of disturbance the diversity in an affected area is low, whilst diversity is high at intermediate levels of disturbance (Petraitis *et al.* 1989, Caswell & Cohen 1991, Rosenzweig 1999). Areas where disturbance occurs often accumulate few species as the disturbance event is experienced more than once within the life span of the resident fauna, thus diversity is kept low and the area is depauperated. Areas where disturbance occurs rarely however, develop intricate biotic interactions where competition excludes species, leading to a low diversity, mature and impoverished community (Deslow 1985, Huston 1994, Valiela 1995, Rosenzweig 1999). The dynamic equilibrium hypothesis suggests that biological diversity is maintained in dynamic equilibrium through the balancing of the opposing processes of disturbance and competitive exclusion (Huston 1979)). Thus, disturbance theory incorporates intermediate, non-equilibrium and equilibrium hypothesis for production and maintenance of diversity (Figure 1.1). Whatever its size and origin, disturbance can be a source of heterogeneity affecting the spatial and temporal occurrence and composition of marine communities (Connell & Keough 1985, Picket & White 1985, Sousa 2001).

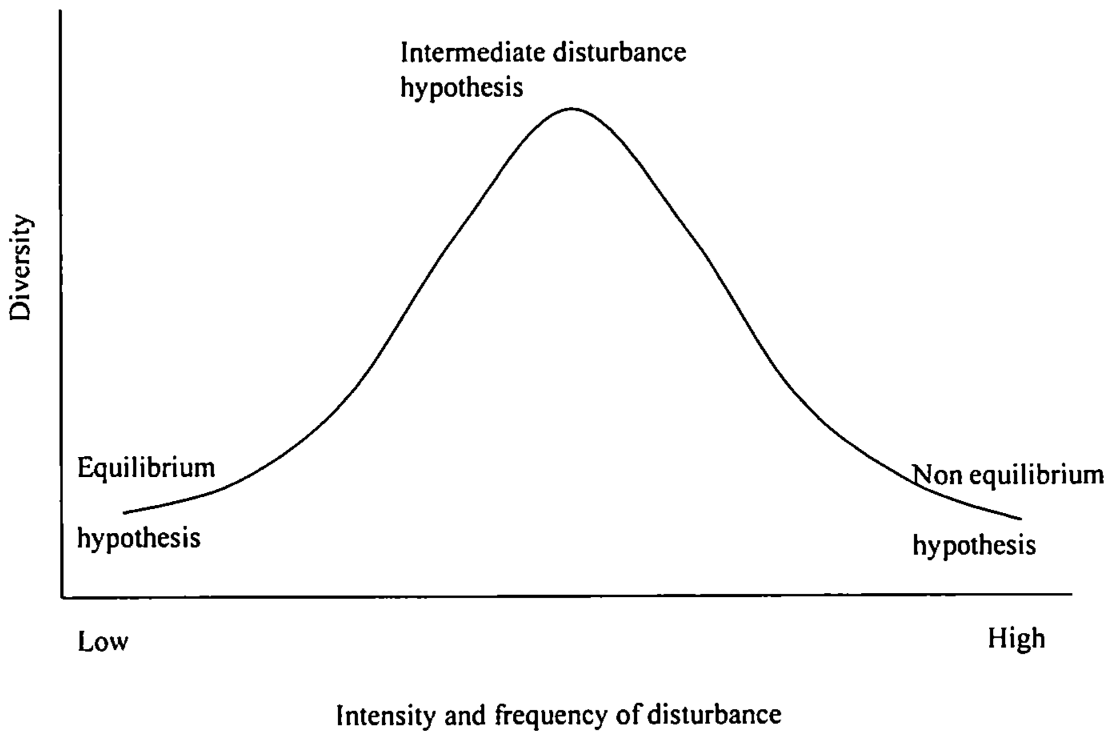


Figure 1.1 Conceptual model of production and maintenance of diversity of species by disturbance (from sources quoted in the text)

In the marine environment frequent wave action at a relatively low intensity, produces disturbance at small spatial scales in intertidal communities (Sousa 1985). Sousa's work on overturned intertidal boulders provided evidence for the links of natural disturbance and biological interactions as processes for maintaining diversity through physical removal of species, predation and space provision (Sousa 1979). Relatively high intensity, regular winter storms produce disturbance at scales of metres to kilometres on subtidal kelp communities through destruction of the algae canopy, with a patchy effect in relation to depth and a cascade of effects in biotic interactions between understorey species (Dayton & Tecner 1984). In contrast, relatively high intensity stochastic disturbances such as hurricanes cause severe structural changes at the ecosystem scale in mangroves and coral reefs (Brown 1997, Lathiresan & Bingham 2001), by opening space and modifying resource availability (e.g. nutrient release from the substrate). Similarly, the inter-link between physical and biological disturbances in kelp communities has been observed as a consequence of El Niño Southern Oscillation (ENSO). Unusually severe storms resulting from ENSO combined with a depletion of nutrients in warm waters can reduce the extent of *Macrocystis* canopy. In certain cases, fish habitat is eliminated and in the absence of predators, amphipods grazed heavily on remaining kelp and other algae (Barry & Dayton 1991, Dayton 1994).

Impact of disturbance on soft-sediment benthic communities

Natural disturbance

Natural physical disturbance has been recognised as a force structuring marine subtidal soft bottom communities (Jones 1950, Grassle & Sanders 1973, Warwick & Uncles 1980, Olafsson *et al.* 1994, Fromentin *et al.* 1997). In a review of disturbance, sediment and trophic structure of soft bottom benthos, Probert (1984) noted that sediment re-suspension caused by winter storms or internal waves can transport passively (or even kill) benthic infauna of continental shelf environments, altering the numbers and biomass and consequently the community structure. Hall (1994), in his later review of physical disturbance and benthic communities, also remarked on the role of disturbance from storms in structuring benthic infauna, but noted that this influence was depth-limited. Emerson (1989) tested the hypothesis that wind stress (resulting from storms) is a limiting variable for benthic secondary production within areas of <20m water depth, reporting that 90% of the variation in total benthic secondary production can be explained by wind variables. Physical disturbance by storms coupled with the general hydrodynamic regime has also been linked to changes in sediment structure and food supply, restricting or modifying animal-sediment interactions (Snelgrove & Butman 1994). However, contrary to such perceived negative impacts (see also Rodriguez *et al.* 1994 and Tilmant *et al.* 1994) storms can promote benthic-pelagic coupling and enhance food supply from the water column, which is reflected in an increase of benthic secondary production (Dagg 1988, Ritzrau & Graf 1992).

Changing sediment characteristics, specifically increasing deposition of fine sediment particles, are generally thought to be responsible for successional changes observed in macrobenthic communities (Aller & Aller 1986, Alongi 1989b, Zajac *et al.* 1998). Periodically, increased river runoff due to heavy precipitation events, can transport fine sediments far out onto the continental shelf. For example, Drake (1999) identified a layer of 5 to 9 cm of fine sediment on the Californian shelf after a flood event. Such changes in the physical characteristics of the sediment are often concomitant with changes in water depth (Gray 1981, Aller & Stupakoff 1996). Increasing depth and decreasing sediment particle size across continental shelves can be coincident with a decrease in the content and quality of sedimented organic material as distances from organic sources (primarily rivers and the euphotic zone) are increased (Dauwe *et al.* 1998). The combined effects of these factors have previously been evoked to explain differences in benthic community structure of continental shelves (Rossenberg 1995, Karakassis & Eleftheriou 1997, Flach & Thomsen 1998).

Large-scale spatial-temporal climatic phenomena such as the 'North Atlantic Oscillation' (NAO) and ENSO can be viewed as having a disturbance effect on the composition, density and biomass of soft bottom benthic communities. Long-term changes in community structure of the benthos in the North Sea and coastal waters of Peru apparently relate to variations in sea surface temperature, precipitation, river runoff and concomitant changes in depth of thermocline, oxygen levels and primary production (Tarazona *et al.* 1988a, 1988b, Kroncke *et al.* 1998, Tunberg & Nelson 1998, Hagberg & Tunberg 2000). Primarily, NAO and ENSO events influence pelagic-benthic coupling relationships, altering the structure of benthic communities through changes in the availability of food as primary production (Buchanan & Moore 1986, Pearson *et al.* 1986, Alongi 1990).

Anthropogenic disturbance

Human disturbance can also modify benthic habitat and food availability. The magnitude of the observed changes depends not only upon the disturbance intensity, frequency and size of area acted upon, but also the differential response of fauna to any background natural disturbance (Lewis 1982, Gee *et al.* 1985, Kaiser 1998, Karakassis *et al.* 2000). Pollution (as defined by GESAMP in Clark 1997) effects according to Gray

(1979, 1981, and 1982) can be divided into disturbance and stress. Disturbance implies the destruction or removal of individuals from an area. Stress, on the other hand, reduces the productivity of an individual. Gray proposes four types of adaptive strategies of infauna to pollution (Figure 1.2).

	low stress	high stress
low disturbance	competitive (K)	tolerant (T)
high disturbance	reproductive (r)	non viable

Figure 1.2 Adaptative strategies of infauna to pollution according to Gray (1979)

Anthropogenic organic enrichment of sediment, for example, has frequently been shown to influence the composition of benthic communities. For example, disturbance effects have been observed as a result of organic inputs from sewage outfalls (Swartz *et al.* 1986, Anderlini & Wear 1992, Ismail 1992), fish farming (Chivilev & Ivanov 1997, Mazzola *et al.* 2000), and paper milling (Millner 1980, Pearson 1980). Organic enrichment causes changes in oxygen levels and depth of the oxidised layer with related chemical changes in interstitial water (Swartz *et al.* 1985, Stull *et al.* 1986). Pearson and Rosenberg (1978) described a model of benthic community response to a gradient of organic enrichment where a succession (both spatially and temporally) of 'community stages' could be identified between extremes of normal and azoic conditions. Those extremes exemplify the adaptive strategies to pollution as proposed by Gray (see above) where competitive dominants exist under normal conditions of low levels of disturbance and stress. On the contrary there are no organisms able to exist under conditions of high levels of disturbance and stress.

Mechanical disturbance causes physical alteration of sediment structure, for example by removing or adding certain size particles (Messieh *et al.* 1991, Newell *et al.* 1998).

Sediment re-suspension by large cruise liners can influence benthic communities by displacing or favouring fauna of certain mobility or feeding guilds (Warwick *et al.* 1990c). Subtidal dredging for sand and gravel extraction physically alters the benthic habitat and can totally remove the fauna (Kenny & Rees 1996, Desprez 2000), and subsequent increases in opportunist species have been observed (Dalfsen *et al.* 2000, Sarda *et al.* 2000). Demersal fishing is perhaps the most pervasive mechanical disturbance operating on continental shelves, where it affects the ecological organisation of benthic communities (Watling & Norse 1998, Bergman & Lindeboom 1999, Frid *et al.* 2000, Kaiser 2000). Not only are benthic organisms affected through the physical alteration of their habitat (Collie *et al.* 2000), but fishing disturbance also alters community structure via elimination of large taxa by direct mortality (Ball *et al.* 2000, Smith *et al.* 2000). Additionally, increased availability of food, as a result of such mortalities, can influence the number of scavengers exploiting the resource (Engel & Kvitek 1998, Ramsay *et al.* 2000, Sanchez *et al.* 2000).

Organic enrichment and physical substrate alteration can be combined in single disturbance events such as sewage sludge dumping (Lear & O'Malley 1983, Pearson 1987, Rees *et al.* 1992), oil spills (Southward 1982, NAS 1985, Davies & Wolff 1990, Davies *et al.* 1997), and disposal of oil/gas drilling material (Dicks & Hartley 1982, Neff *et al.* 1989, Daan & Mulder 1996a). Such disturbances have additional impacts on benthic communities through the release of pollutants (Anderson *et al.* 1974, Somerfield *et al.* 1994, Herrando-Perez & Frid 1998), changes in chemical properties of interstitial water and increase in suspended solids concentrations (Oostdam, 1983).

Oil-spills can smother and destabilise sediment, particularly in intertidal and shallow subtidal habitats (Sanders *et al.* 1980, Jackson *et al.* 1989, Dean *et al.* 1996, Peterson 2001). Depending on the magnitude of the oil spill and the prevailing physical setting and weather conditions of the area, an immediate severe impact is observed with a variable recovery from 1 to 10 years (Elmgren *et al.* 1983, Dauvin 1998, Guidetti *et al.* 2000). Subtidal habitats deeper than 10 metres are less affected due to prevention of oil sedimentation, oil weathering, and the inherent physical characteristics of the substratum in relation to natural disturbance regimes (Kingston *et al.* 1995, Jewett *et al.* 1996, Lee & Page 1997, Feder & Blanchard 1998). For example, after the *Amoco Cadiz* oil spill, communities of muddy fine-sand substrates were more affected than communities of sandy substrates, the latter being presumably more adapted to physical disturbance (Dauvin 1982, Dauvin & Gentil 1990). Following the initial acute impact, opportunistic species responded promptly to the organic enrichment by increasing in numbers, in contrast to the disappearance of species sensitive to oil toxicity (Sanders *et al.* 1980, Dauvin 1982).

Drilling fluids and cuttings that result from offshore oil and gas extraction activities are disposed of on many continental shelves throughout the globe (Flood 1992, Steinhauer *et al.* 1994, Daan & Mulder 1995, Patin 1999, Rezende *et al.* 2002). The main consequence in terms of impact on the benthos is that such drilling materials are of high specific gravity and are discharged in large quantities. Therefore, they deposit on the seabed in the vicinity of each site of drilling activity (Menzie 1982, Gillmor *et al.* 1985, Grant & Briggs 2002, Holdway 2002) rather than dispersing in the water column. Three main effects have been recognised from these discharges: smothering, toxicity and organic enrichment (Addy *et al.* 1984, Kingston 1987, Daan *et al.* 1990). Generally such disturbance is considered to be local, with a clear gradient of influence away from the site of oil drilling/extraction. Up to 200 m from the drilling/extraction site the sediment is azoic, 200-750 m distant an impoverished and highly modified community exists, whilst between 750-2000 m, high densities of opportunistic species occur in an area of organic enrichment. This latter area represents a transition zone to areas beyond which alterations in the community are usually undetectable (Davies *et al.* 1984, Mair *et al.* 1987, Moore *et al.* 1987, Daan *et al.* 1992, Kingston 1992). However, other evidence points towards an extended area of influence up to 6000 metres away from the source following the main direction of residual currents, and a regional rather than local approach has been proposed when addressing oil related impacts from offshore activities (Gray *et al.* 1990, Olsgard & Gray 1995). There are some examples where no impact or related gradient of fauna response to oil activities has been found (Pogrebov *et al.* 1997, Windom & Cranmer 1998) or where trophic relations within particular taxa seemed not to be affected (Maurer *et al.* 1981). Nonetheless, disturbances from offshore oil and gas activities are thought to have long-term effects on benthic community composition (Dicks & Hartley 1982, Boesch *et al.* 1987, Daan & Mulder 1996b). However, describing and understanding the disturbance effects of oil extraction activity on benthic macrofauna communities is particularly difficult as it will depend on the history of exploitation, type of discharges, environmental setting and background natural disturbance (Lewis 1982, Bakke *et al.* 1989, Neff *et al.* 1989, Pearson & Mannvik 1998, Patin 1999).

The Gulf of Mexico

The Gulf of Mexico (GoM) (Figure 1.3) is categorised as a small ocean basin with total surface area of ~ 1.5×10^6 km^2. The Gulf's continental shelf extends out to water depths of 100 to 200 m before the slope descends to a central plain of 3700 m of maximum depth. Shelf width has a maximum of about 280 km off the Florida and Yucatan Peninsulas and a minimum of 10 km adjacent to the Mississippi Delta. The shelf is comprised of a massive carbonate platform in the south and east, and a thick embankment of terrigenous sediment in the north and west. The Gulf's abyssal plain is levelled with sediments of terrigenous origin except for some diapiric salt structures named the Sisgbee knolls. (Uchupi 1975, Martin & Bouma 1978, Rezak *et al.* 1985, Vidal-Lorandi *et al.* 1999). Physiographically the Gulf is divided as follows: 1) the Gulf basin or Sigsbee plain, 2) west Florida carbonate platform and slope, 3) Mississippi-Alabama shelf and slope, 4) Texas-Louisiana shelf and slope, 5) east Mexico shelf and slope, 6) Campeche Bay or saline basin of Mexico and 7) the carbonate Campeche Bank or Campeche shelf (Antoine 1972, Martin & Bouma 1978).

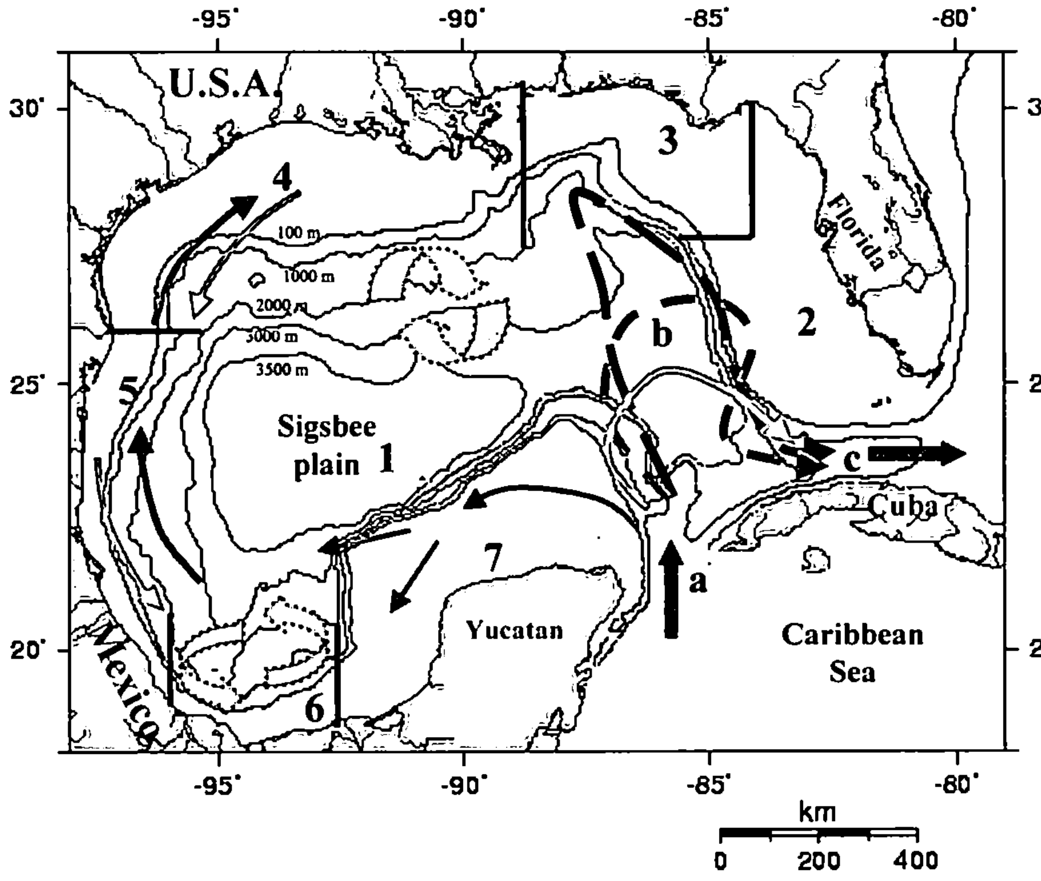


Figure 1.3. Map of the Gulf of Mexico showing bathymetry, major water currents and physiography. Light grey arrows refer to winter circulation, and dashed broad arrows show areas of cyclonic and anticyclonic circulation. Letters a-c refers to the Yucatan current, Loop current and Florida Current respectively showing temporal variation of Loop current penetration (see text for explanation). Numbers 1-7 refer to physiographic provinces (From sources quoted in the text).

The general water circulation patterns of the Gulf (Figure 1.3) are driven by the northward flow of the Caribbean Current that enters through the Yucatan Channel (named Yucatan Current). From here the current migrates towards the northern-central area of the

Gulf before turning down along Florida shelf (named the Loop Current) and finally exiting through the Florida Straits (named Florida Current) (Rezak *et al.* 1985, Biggs *et al.* 1998, Martinez-Lopez & Pares-Sierra 1998). The Loop Current influences the outer shelf circulation of the entire Gulf either by direct intrusion, that reaches its maximum in late summer (Huh *et al.* 1981, Molinari & Morrison 1988), or by anticyclonic rings that detach from it at least once a year (Elliot 1982). The detached rings travel westward and can collide onto the western continental slope which, together with the wind forcing, controls the circulation along the western boundary of the Gulf (Merrell & Morrison 1981, Sturges 1993, Vidal *et al.* 1999).

The Gulf comprises five water masses between a depth of 2000 m and the surface. These are in order of decreasing depth, the North Atlantic Deep Water, The Caribbean Intermediate Water, The Tropical Atlantic Central Water, The Caribbean Subtropical Underwater and The Gulf Common Water. Horizontal variations of sea surface temperature and salinity in the Gulf range in average from 19° - 20° C and 32 -32.4 ‰ in the north-eastern region to 24° -25° C and 36.4 - 36.6 ‰ in the south-east region of the Gulf (Caruthers 1972, Nowlin 1972, Vidal *et al.* 1994).

There are major seasonal variations in the vertical characteristics of the water masses of the gulf. Vertical stratification builds up during summer as a consequence of the constant freshwater input from rivers, and heating during periods of southerly and south-easterly trade winds. Stratification is destroyed during autumn and winter (October to March) by northerly cold-air outbreaks called 'northers', (peak intensity of 90 to 110 km/h and 1 to 5 days of duration, (Salas de Leon *et al.* 1992, Boicourt *et al.* 1998, Magaña *et al.* 2001)). Northers are the main large-scale natural disturbance of the Gulf, with residual currents transporting sediment across the shelf and beyond the continental slope (Shideler 1981, McGrail & Carnes 1983). Such physical disturbance is known to affect shallow bottom communities on the northern Gulf (Dagg 1988, Thistle *et al.* 1995, Posey *et al.* 1996). The other natural disturbances that potentially influence benthic communities throughout the region are delivered from the main large rivers that enter the Gulf. Such disturbances are more localised and of more variable influence. For example, the Mississippi river introduces sediment washed from agricultural areas which, during the peak of the rainy season, is thought to be responsible for eutrophication and related hypoxia-anoxia conditions observed over large areas of the adjacent shelf (Harper *et al.* 1981a, Harper *et al.* 1991, Rabalais *et al.* 1991). Hurricanes represent another disturbance event that can occur in the Gulf region (with wind intensities on the order of 120 km to 200 km/h); however such events occur less frequently and influence turbidity and nutrient loading inside and outside the area of direct impact (Tilmant *et al.* 1994, Bayazitoglu 2000).

Anthropogenic disturbance of the Gulf's benthic habitats is significant in areas where agriculture, urbanisation and industrial development have contributed to substantial coastal degradation and precipitated the supply of sediment and pollutants onto the continental shelf (Sackett 1981, Trefry *et al.* 1985, Gold Bouchot *et al.* 1999, Rivera-Arriaga & Villalobos 2001). Trawling by the extensive shrimp fishery on areas of the northern and southern Gulf disturbs the seabed and the shelf communities (Gracia & Vazquez Bader 1999, Patillo & Nelson 2000). However, activities related to the extraction and transportation of oil and gas are considered the greatest human-related disturbance threat to the region (Giammona & Darnel 1990, Sherman 1994). The extensive research in the Buccaneer gas and oil field of the northern Gulf demonstrated a range of local impacts on the benthic ecosystem (Middleditch 1981a and papers therein). Field and experimental studies continue on the effects of drilling discharges and produced water on the benthic fauna (Sharp & Appan 1982, Capuzzo 1987, Neff *et al.* 1987) as well as monitoring of long-term chronic impacts (Giammona & Darnel 1990, Kennicutt *et al.* 1996b, Montagna & Harper 1996).

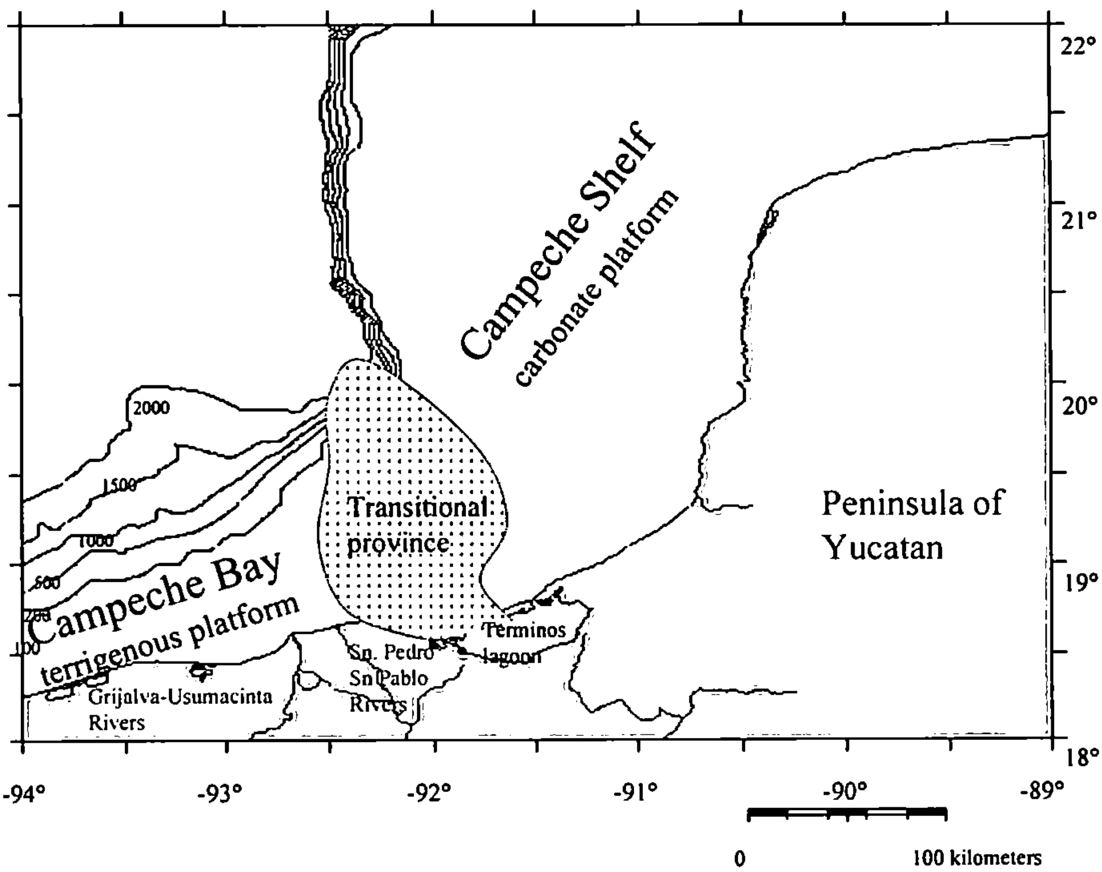


Figure 1.4. The Southern GoM including the Campeche Shelf and Campeche Bay provinces together with the transitional sedimentary province of mixed carbonate and terrigenous sediments and the major fluvial systems.

The Southern Gulf of Mexico and the Campeche Bay and Shelf

The southern GoM includes the Campeche Shelf and Campeche Bay (Figure 1.4), a large continental shelf environment that is subject to a number of natural and human disturbances. Shelf width ranges from 220 km at its northern part and 37 km at its south-western region (Campos-Castan 1981). The northern part of the Campeche shelf, along most of the coast of the Yucatan Peninsula, is composed of a carbonate platform characterised by a gentle slope and irregular bottom, with sandbanks, coral reefs and biogenic sediments (Logan *et al.* 1969, Rezak & Edwards 1972). The water column over this section of the shelf is considered vertically uniform, with high salinity and density due to high evaporation and the lack of superficial river runoff (Monreal-Gomez *et al.* 1992). The shelf narrows towards the Campeche Bay in the south-west; consequently the slope steepens and the sedimentary features of the shelf are terrigenous with a very fine mud and clay bottom (Bouma 1972, Campos-Castan 1981). It is presumed that this area of the shelf has persistently turbid bottom water (similar to its northern counterpart off Louisiana and Texas) resulting from the influence of the adjacent fluvial systems of the Grijalva-Usumacinta, San Pedro-San Pablo rivers and Terminos Lagoon (Rezak *et al.* 1985, Rezak *et al.* 1990). A transitional, or mixing, shelf province has been recognised between the northern (carbonate shelf) and south-western (terrigenous shelf) provinces of the Campeche Shelf and Bay. Different levels of carbonate content ranging from 25 to 75% have been proposed to differentiate this broad transitional shelf province (Yañez-Arancibia & Sanchez-Gil 1983, Carranza-Edwards *et al.* 1993, Carranza-Edwards *et al.* 1996).

A branch of the Loop Current drives the water circulation of the southern GoM, with a west to south-west flow during spring and summer (Figure 1.5a) and an east to north-east flow during late autumn and winter (Figure 1.5b) (Boicourt *et al.* 1998, Martinez-Lopez & Pares-Sierra 1998). The maximum intrusion of the Loop Current into the GoM is thought to be responsible for the presence of a large cyclonic ring in the Campeche Bay area from August to March (Monreal-Gomez & Salas-de-Leon 1985). Late-spring field observations have corroborated the presence of the cyclonic gyre and its interaction with river runoff on the southern part of the Campeche Bay (Padilla-Pilotze *et al.* 1990).

The main natural disturbances in the southern GoM are the 'northers' and river runoff. Both these forces strongly influence the shelf's sedimentary environments and modify the extent of the transitional shelf province (Yañez-Arancibia & Sanchez-Gil 1983), thereby driving ocean-shelf-coastal interactions in the region (Fuentes-Yaco *et al.* 2001). From October until March, 'northers' produce vertical mixing of the previously stratified water column, and sediment re-suspension on shallow areas of the shelf, and this has a seasonal influence on benthic pelagic-coupling (Escobar-Briones & Soto 1997). Such disturbances are thought to be responsible for observations of temporal variation in secondary production (Soto & Escobar-Briones 1995). Riverine influences on the shelf of the southern GoM are considered a permanent feature (Monreal-Gomez *et al.* 1992). Average freshwater discharge from the Grijalva-Usumacinta River alone has been estimated at 2.13 x 10^3 m^3 s^{-1}, with peak discharges during the rainy season from July to September/October (CNA 2001). River runoff represents the main supply of sediment load and associated organic material (Hedges & Parker 1976, Hedges & Mann 1979), which influences the diversity of benthic megafauna across the terrigenous shelf province of the Campeche Shelf and slope (Soto *et al.* 1998).

Important economic activities, such as a pennaeid fishery and oil production, take place on the south-western portion of the Campeche Shelf (Figure 1.5). Shrimp trawling in the southern GoM has been demonstrated to affect non-target benthic species and possibly impact the biodiversity of the region; however, the exact level of disturbance has not been assessed (FAO 2000). Offshore oil and gas activities have developed since 1974 in the transitional area of the Campeche Shelf. The region is the largest offshore oil production centre in Mexico. It comprises a delimited polygon (Figure 1.5) with an area of 8,000 km^2 that contains more than 200 platforms and in which fishing and other non oil-related commercial activities are forbidden (Santiago & Baro 1992, Valdes & Ortega-Ramirez 2000, PEMEX 2001). Potentially these platforms (and related transport activities) are the main contributor to the hydrocarbon load of recent sediments (Botello *et al.* 1991, Gonzalez *et al.* 1992, Vazquez-Botello *et al.* 1993). The blow out of the Ixtoc-I well in 1979 produced awareness of the potential risks of offshore oil activities, the role of ocean currents in the dispersal of the spilled plume, and the mechanism by which oil sedimentation took place and thereby influenced the benthic compartment (Boehm & Fiest 1982, Boehm *et al.* 1982). However, little has been done to assess the effect of disturbance on benthic communities, despite the effort applied to understanding the large scale ecological processes of the southern GoM (Yañez-Arancibia & Sanchez-Gil 1983, Granados-Barba & Solis-Weiss 1997, Manickchand-Heileman *et al.* 1998, Vazquez *et al.* 2000).

Study aim

The overall aim of the present study was to investigate the influence of natural and anthropogenic disturbances, represented by events associated with the major climatic periods and offshore oil related activities, on the macroinfauna communities of the Campeche Shelf, southern GoM. The overall aim will be deconstructed into separate testable hypothesis presented in the following chapters. Chapter 2 will present a preliminary broad scale (>100 km) sampling survey to explore for spatial and temporal differences in community composition between two sedimentary environments as a result of winter storms and seasonal river runoff. Chapter 3 will examine the impact of natural disturbance from river runoff and winter storms at a smaller scale of tens of kilometres. Chapter 4 will assess in detail the influence of oil related impacts on the benthic communities and if it is possible to differentiated from natural disturbance. Chapter 5 will give a full discussion of the findings and present a series of conceptual models of the interaction of disturbance factors and the benthic macroinfaunal communities.

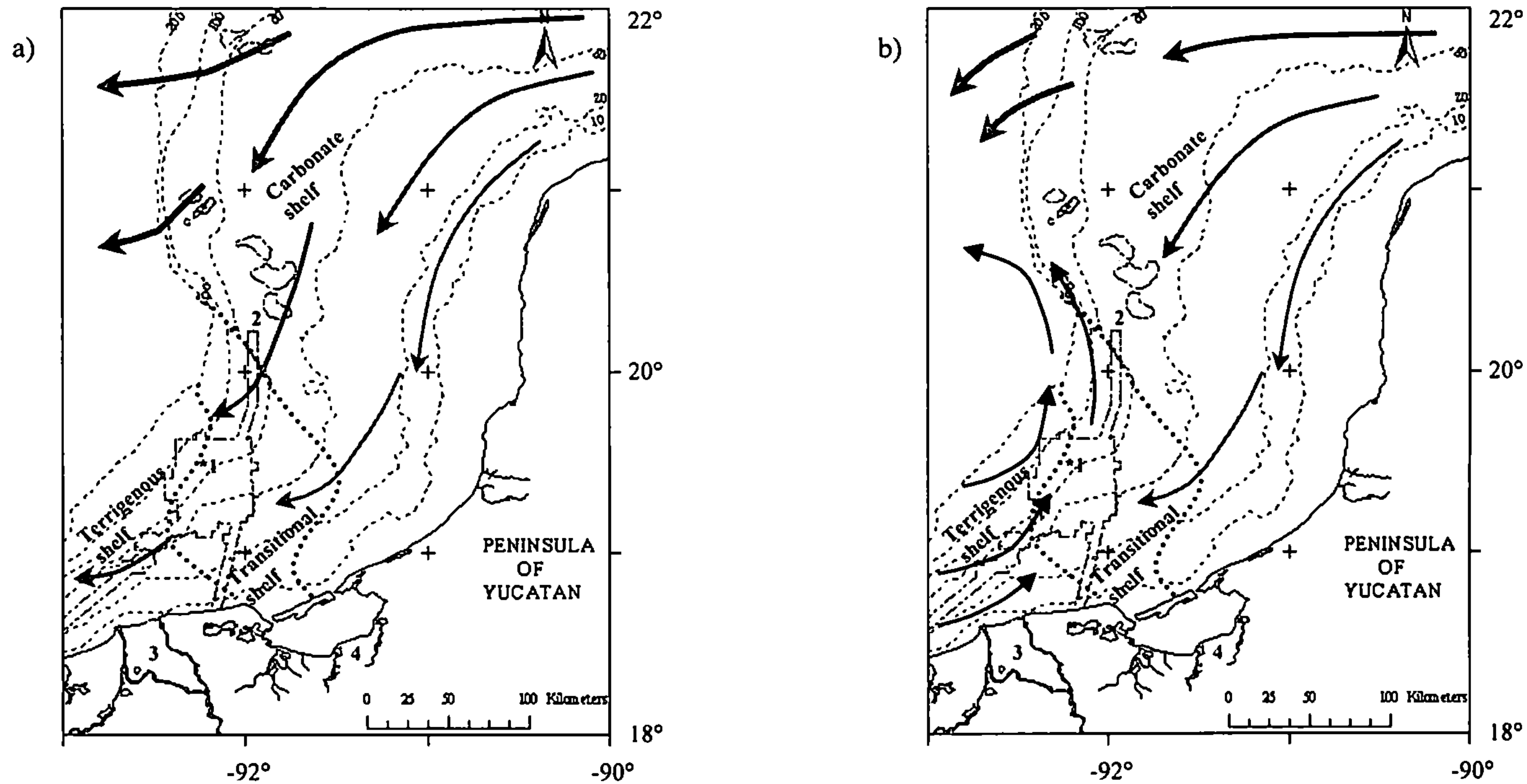


Figure 1.5. Maps of the Campeche Shelf in the Southern GoM showing the bathymetry, shelf provinces and major current patters in a) spring-summer (light arrows) and b) late autumn-winter (light arrows represent the Yucatan Current influence and dark arrows thecournter current influenced by the cyclonic gyre). Numbers indicate 1) Area of offshore oil activities (*Ixtoc 1 well) and submarine pipe lines, 2) Main loading port for oil tankers, 3) Grijalva-Usumancinta and San Pedro-San Pablo river system and 4) Terminos lagoon runoff system.

CHAPTER 2

PRELIMINARY INVESTIGATIONS INTO THE BENTHIC MACROINFAUNA OF THE SOUTHERN GULF OF MEXICO

Introduction

Communities of benthic macroinfauna on the continental shelves of the GoM are thought to be structured by a mosaic of sediment types, together with depth related factors such as bottom water stability and food supply (Alexander *et al.* 1981, Darnell 1990, Rabalais *et al.* 1999). Studies to date reveal that inner shelf (<30m water depth) macroinfauna communities on the eastern, mainly carbonate, shelf of the Gulf are consistently diverse, with species numbers greater than 400 being recorded for the area (Phillips *et al.* 1990, Posey *et al.* 1998). Community structure on the northern shelf is more variable, with species numbers ranging from 60 to 300 for the area in response to environmental instability and muddy to sandy sediments (Flint & Holland 1980, Flint & Rabalais 1980, Rabalais 1990). Bottom water instability at water depths <30m is closely related to natural disturbances such as winter storms (Fanning *et al.* 1982), river runoff (Murray *et al.* 1982) and seasonal hypoxia (Harper & Guillen 1989). Winter storms resuspend and transport macroinfauna (Oliver *et al.* 1980, Okey 1997) and cause differential mortality of suspension feeding macroinfauna (Eagle 1975, Posey *et al.* 1996). Hypoxia as a result of heavy river runoff causes dramatic reductions of between 50 and 80% in macrobenthos densities and species numbers (Harper *et al.* 1981b, Gaston 1985, Harper & Guillen 1989, Harper *et al.* 1991). In contrast, outer shelf environments (>50m water depth to the shelf break) are more stable and harbour a diverse community with low densities (Flint & Holland 1980, Phillips *et al.* 1990).

The macroinfauna communites of the continental shelves in the western and southern Gulf have been less studied than their northern and eastern counterparts. However, it has been established that two major meteorological periods, namely the rainy and winter storms (northers) seasons, drive the ecological structure of the area (Yañez-Arancibia & Sanchez-Gil 1983, Fuentes-Yaco *et al.* 2001). It has been proposed that benthic biomass on the terrigenous inner and middle western and southern shelves is enhanced by organic inputs from river runoff during the rainy season and reduced by physical disturbance during the winter period (Soto & Escobar-Briones 1995, Escobar-Briones & Soto 1997). Similar to the other shelf areas of the Gulf, benthic biomass decreases with increasing depth and its spatial and temporal variability is related to sediment structure and the local hydrodynamic regime (Soto *et al.* 1998). The few studies that exist for the southern Gulf indicate that the macroinfauna community is likely to have as high a species number and diversity as that observed for the eastern Gulf. For example, taxonomic studies on polychaetes (the dominant macrofauna of the GoM's shelf communities) of the southern Gulf have reported 135 species (Granados-Barba 1994, Granados-Barba & Solis-Weis 1998) which compares with 213 species of polychaetes from the carbonate shelf off Florida (Posey *et al.* 1998). The few ecological studies of the Southern GoM have been based mainly on the areas of the shelf directly influenced by river runoff, but still provide a framework and baseline for examining the structure and function of this large shelf system (Rabalais *et al.* 1999). They also highlight the need for ongoing research on the benthic ecology of the region, in particular a description of 'whole' benthic communities, and their responses to prevalent natural disturbance for the area is of economic importance in terms of fishing and offshore oil extraction (Vazquez *et al.* 2000, Gracia & Vazquez Bader 1999).

In 1993, a joint research program between CINVESTAV (Mexico) and the KBIN (Belgium) commenced on the shelf of the southern GoM. This aimed to describe the meiobenthic community structure in relation to sediment patterns and oil related activities (Fiers 1996). The opportunity was taken to extend the scope of the study by incorporating a survey of the macroinfauna of the area (Hernandez-Arana 1995, Sanchez-Garcia 1995). A subset of the data from the macroinfauna survey provided the present opportunity to specifically explore potential reasons for any observed differences in community composition between two areas of the shelf, and changes that might occur in community composition between seasons, which could represent differences in spatial and temporal natural disturbance. Specifically, the aim of this study was to test the hypothesis that there is a difference in macroinfauna community composition between the two sedimentary environments of the southern GoM, and that any differences observed in composition vary with depth and season.

Materials and methods

Study site

The Campeche Shelf in the southern GoM, is a broad platform with a gentle slope, ranging in width from 220 km at its northern part to 37 km at the southern extreme (Campos-Castan 1981) (Figure 2.1). The study site is divided into two areas that represent different sedimentary environments (Gutierrez-Estrada & Galaviz-Solis 1991). The shelf's northern portion is a carbonate environment, characterised by numerous banks and shallows with coarse sediments and a high carbonate content (>75%) of autochthonous origin (Logan *et al.* 1969, Wartel & Salinas 1996 in Fiers 1996). The southern part is a transitional, or mixed, carbonate-terrigenous environment, with a carbonate content that ranges from 25 to 75%, influenced by river runoff from the Grijalva-Usumacinta River system (Bello & Cano 1991, Carranza-Edwards *et al.* 1993, Aguayo-Camargo *et al.* 1999)

There are three main climatic periods in the southern Gulf: 1) Dry from February/March to June, which corresponds to the minimum river discharge and is dominated by easterly trade winds (Boicourt *et al.* 1998, CNA 2001). 2) Rainy from June/July until September with two peaks of maximum precipitation which correspond to maximum river discharge and continuous influence of easterly winds (CNA 2001, Magaña *et al.* 2001). 3) 'Northers' or cold fronts from October to March that may extend until April, typically with 15-27 cold outbreaks with a north to north-east direction and wind speed ranging from 21 to 30 m/s for 3-5 days of duration at any one time (Salas de Leon *et al.* 1992, Magaña *et al.* 2001). During the dry and rainy season, the general water circulation pattern has a west to south-west flow driven by a branch of the Loop Current (Boicourt *et al.* 1998, Martinez-Lopez & Pares-Sierra 1998), which persists all year across the northern carbonate region. On the southern part of the shelf, frontal interactions occur between river discharges and oceanic water (Czitrom *et al.* 1986, Carranza-Edwards *et al.* 1993). At the end of the rainy, and during the northers season, the flow reverts from east to northeast on the southern part, due to both the formation of a cyclonic ring on the Campeche Bay (Monreal-Gomez & Salas-de-Leon 1990) and the interaction with the southward flow from the western Gulf (Boicourt *et al.* 1998).

Study design

Samples from two surveyed transects which crossed the transitional and carbonate environments of the Campeche Shelf were utilised for the present study (Fiers 1996).

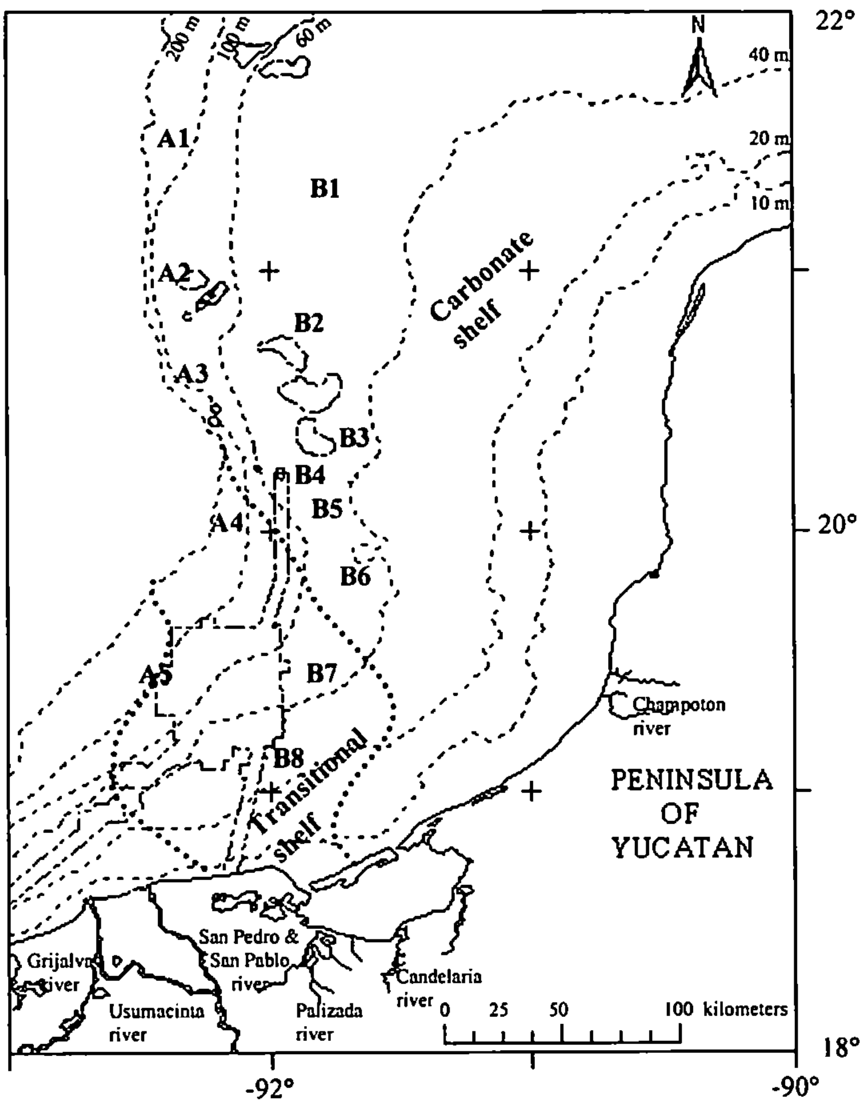


Figure 2.1. A map of the Campeche Shelf in the southern GoM showing the spatial location of stations sampled for macroinfauna in 1993. Sites A1-A3, B1-B6 correspond to the Carbonate environment; whilst stations A4, A5, B7, B8 represent the transitional shelf environment.

Transect A ran approximately north to south from 80m to 170m water depth, whilst the parallel transect B went from 20m to 50m water depth. Five and eight sampling stations were positioned along transects A and B respectively. The two most southern stations of each transect were deemed to represent the transitional environment and the remaining nine, the carbonate environment of the shelf. In order to investigate the influence of temporal disturbance, the design includes sampling after the three main climatic periods, namely "northers", dry and rainy seasons.

Sampling methodology

Sampling was carried out from an ocean-going research vessel in 1993 after the winter storms (or "northers") season (27^{th} February - 6^{th} March), after the dry season (28^{th} June – 4^{th} July), and after the rainy season (22^{nd} - 28^{th} October). Stations were located and positioned using the satellite navigation system of the research vessel (Appendix 1). The thirteen stations were sampled in triplicate using a box corer (Hessler Sandia MKII type, 40 x 40 x 40 cm capacity). Infauna was sampled using sub-cores of 0.05 m^2 x 20 cm depth from each of the three box cores recovered at each station. Each sub-core was sieved on a 1mm mesh; retained macroinfauna were anhestesied with $Mg Cl_2$, then fixed with 5% formaldehyde solution buffered in seawater and stained with Rose Bengal prior to storage. Separate sub-samples for analysis of organic matter (three per station) and grain size (one per station) were taken using sub-cores of 0.01 m^2 x 10 cm depth from each box core recovered and frozen onboard prior to analysis.

Laboratory analyses

Macroinfauna samples were transferred to a solution of 70% ethanol. Subsequently, organisms were sorted, counted and identified to family level using taxonomic literature available for the GoM (Uebelacker & Johnson 1984, Williams 1984, Kensley & Schotte 1989, Granados-Barba 1994) and from other areas (Lincoln 1979, Holdich & Jones 1983, Barnard & Karaman 1991). Identification of the fauna to family level has been demonstrated to be sufficient in order to assess natural spatial variation and patterns of disturbance in marine macroinfauna (Long & Lewis 1987, Warwick 1988b, James *et al.*

1995, Olsgard & Somerfield 2000). Organic matter was analysed using the wet oxidation technique described in (Holme & McIntyre 1984). Grain size analysis, following the technique described in (Wartel *et al.* 1995) was undertaken separately for 2cm sections of each core, and for the purpose of this study a mean measure for the total 10-cm was calculated for mean grain size (phi units), percentage of sand, silt and clay, and sediment sorting.

Data analyses

Univariate analyses: ANOVA. Three factor ANOVA was undertaken using the number of individuals, number of taxa and Shannon-Weiner diversity index (Log*e*) calculated from each replicate as the response variables, and sediment, depth and seasons as fixed orthogonal factors (NB The factor season is referred to sampling dates and no inference is intended to be drawn in relational to multiyear seasonal variation). A balanced design was constructed with two stations, randomly picked, from each combination of sediment-depth strata from the carbonate sedimentary environment to match the existing four stations from the transitional sedimentary environment (Appendix 2). All data were tested for homocedasticity using Cochran's test and transformed where necessary (Log (x+1)). Analyses were performed using GMAV5 (Underwood & Chapman 1998) for Windows, and guidelines for ANOVA design were taken from Underwood (1997). Significance level was set at $\alpha = 0.05$. Three null hypotheses were tested at the chosen levels of spatial and temporal variation.

a) No differences in average of community measures between the carbonate and transitional sedimentary environments.

b) No differences in average of community measures between deep and shallow water strata.

c) No differences in average of community measures among 'northers', dry and rainy seasons.

Physical disturbance from the 'northers' and rainy season may influence differentially carbonate and transitional sedimentary environments as well as deep and shallow water strata. Therefore first (Sediment x depth, sediment x season, depth x season) and second (sediment x depth x season) order interactions are likely to occur.

Stepwise multiple linear regression analysis was undertaken to explore the relationship between depth, mean grain size (phi units), percentage of clay, sorting of sediment and percentage of organic matter using number of individuals, number of taxa and diversity H'. The aim was to investigate which variables best explained the univariate patterns observed for each season. All community measures were tested for departures from normality using Wilks λ test and log-transformed when necessary (number of individuals only).

Multivariate approach. Multivariate analysis was undertaken by utilising the PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 software package (See Clarke & Warwick 1994, Clarke & Gorley 2001 for details). Using a ranked similarity matrix, based on Bray-Curtis similarity measures of fourth root transformed macroinfauna family data, an ordination plot was produce by non-metric multidimensional scaling (MDS). Formal significance test for differences in similarity in community composition was undertaken using ANOSIM. Due to the restrictions of ANOSIM, which only allows a maximum of 2-factor (Clarke & Green 1988, Warwick *et al.* 1990a), the test for differences was done for a two way layout among four environments or 'blocks' defined by a combination of sediment-depth strata (carbonate-shallow, stations B1-B6; carbonate-deep, stations A1-A3; transitional shallow, stations B7 and B8 and transitional-deep, stations A4 and A5), and three seasons. Interactions were addressed on a formal and indirect approach by the one-way ANOSIM layout (Clarke 1993). Families contributing to any dissimilarity between grouped samples were investigated by the similarity percentage procedure SIMPER (Clarke 1993). The relationship between community structure and environmental variables was examined using the BIOENV procedure (Clarke & Ainsworth 1993) with the same sediment variables as used for the linear regression described above. BIOENV uses a Spearman's Rank Correlation between the resulting ranked similarity matrices of fauna and correlation-based PCA of the normalised environmental variables. variables were checked for co-correlation using Pearson's product moment correlation coefficient. All variables were retained as none had an r-value greater than 0.95.

Results

A summary of data of sediment variables, abundance, number of families and diversity (H'*e*) is presented in Appendices 1 and 2 for each station and season.

Univariate analysis

ANOVA. Differences in mean densities of macroinfauna on the Campeche Shelf were dependent on a combination of sedimentary environment, depth and season. Whilst significant, the influence of each factor was inconsistent, as the highly significant three factor interaction of the following ANOVA demonstrated (Table 2.1).

Table 2.1. Three factor fixed -orthogonal ANOVA model testing for differences and interactions in macrobenthos numbers of individuals, number of taxa and Shannon-Wiener diversity index between two sediment types (carbonate-transitional), two depth strata (deep-shallow) and three seasons (after northers, after dry and after rainy seasons). Heterogeneity in the variances of numbers of individuals and Shannon-Wiener diversity index was not removed by any transformation, so the analyses were therefore run without transformation.

Factor	SS	d.f.	MS	F	P
Number of individuals					
Sediment	1508729	1	1508729	98.98	<0.0001
Depth	1528772	1	1528772	100.29	<0.0001
Season	1606824	2	803411	52.71	<0.0001
Sediment x Depth	533458.4	1	533458.4	35	<0.0001
Sediment x Season	717151.1	2	358575.5	23.52	<0.0001
Depth x Season	538997.9	2	269499	17.68	<0.0001
Sediment x depth x season	**221352.3**	**2**	**110676.2**	**7.26**	**0.0015**
Residual	914601.7	60	15243.36		
Total	7569886	71			
Number of taxa					
Sediment	4826.531	1	4826.531	139.36	<0.0001
Depth	790.0313	1	790.0313	22.81	<0.0001
Season	3564.813	2	1782.406	51.46	<0.0001
Sediment x Depth	**403.7535**	**1**	**403.7535**	**11.66**	**0.0012**
Sediment x Season	**353.3598**	**2**	**176.6979**	**5.1**	**0.009**
Depth x Season	153.5625	2	76.7813	2.22	0.1178
Sediment x depth x season	71.5903	2	35.7951	1.03	0.362
Residual	2078.042	60	34.634		
Total	12241.72	71			
Shannon-Wiener diversity					
Sediment	2.0481	1	2.0481	44.18	<0.0001
Depth	0.5054	1	0.5054	10.9	0.0016
Season	0.6776	2	0.3388	7.31	0.0014
Sediment x Depth	**0.321**	**1**	**0.321**	**6.92**	**0.0108**
Sediment x Season	0.1256	2	0.0628	1.35	0.2657
Depth x Season	**2.1366**	**2**	**1.0683**	**23.05**	**<0.0001**
Sediment x depth x season	0.0965	2	0.0483	1.04	0.3593
Residual	2.7812	60	0.0464		
Total	8.692	71			

The carbonate sedimentary environment had higher densities than the transitional one, but densities tended to be also higher on the shallow strata and much higher in dry and rainy seasons (Figure 2.2a-c). There were no significant differences between the carbonate and transitional sedimentary environments during the 'northers' at either depth level, or between depth strata within the two sediment types. However during the dry season, significant differences were observed between the carbonate and transitional environment only at shallow sites, whilst differences between depths existed over both sediment types. Finally in the rainy season significant differences were present between sediment types at the two depths and between depths within both sedimentary environments.

For number of taxa, two first order interactions were apparent: sediment x depth and sediment x season (Table 2.1), i.e. differences in mean number of families between the carbonate and transitional environments are dependent on both depth and season. A higher mean number of families was observed in the carbonate environment (Figure 2.2d-e), but this was exaggerated at the shallow depths and also during the dry and rainy seasons. Similarly for the Shannon-Wiener diversity index, two highly significant first order interactions were apparent: sediment x depth and depth x season (Table 2.1). Depth, but not season, affected differences in mean diversity between the sedimentary environments, with a higher mean diversity on the carbonated sediment but no differences between depth (Figure 2.2f-g). Similarly, differences in mean diversity between depth strata were affected by season, with a higher diversity in the deeper environments, accentuated in the dry and rainy seasons.

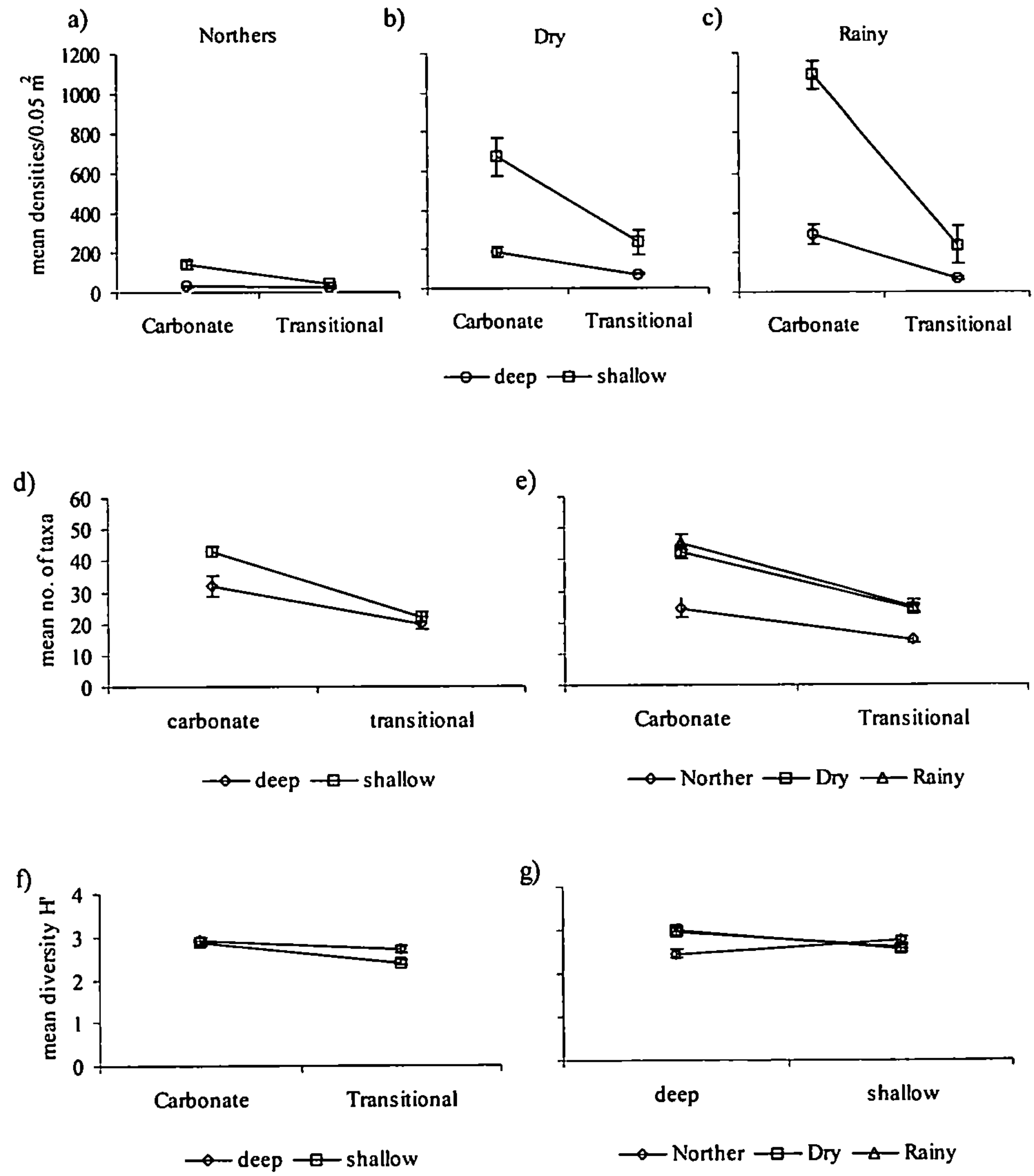


Figure 2.2. Interaction plots of the three factor ANOVA model on effects of sediment type (carbonate, transitional), depth strata (deep, shallow) and seasons ('northers', dry and rainy) on mean abundance, number of families and diversity (H'*e*) of macroinfauna on the Campeche Shelf. (a-c) Second order interaction plots (Sediment x depth x season) on differences in mean densities (No. of individuals/0.05 m^2). (d-e) First order interaction plots (sediment x depth and sediment x season) on differences in mean number of families. (f-g) First order interaction plots (sediment x depth and depth x season) on differences in mean diversities (H').

Table 2.2. Best-fit models from the stepwise multiple linear regression analysis performed on average data per station of number of families without transformation and average data of log number of individuals of macroinfauna for each sampled season.

Northers Season (n=12)	**Number of taxa**		**Number of individuals**	
Predictor variables	Coefficient	P-value	Coefficient	P-value
Constant	25.7325	0.0001	4.99086	0.0000
MGS (phi)	0.18316	0.026		
% Clay	-0.25336	0.0345	-0.03597	0.004
Regression		0.003		0.004
R-square	0.7243		0.58	
Dry Season (n=12)				
Constant	50.3541	<0.0001	7.19658	0.0000
% organic matter	-20.5543	0.0275	-1.4384	0.0209
Depth			-0.008	0.021
Regression		0.0275		0.0051
R-square	0.3992		0.6912	
Rainy Season (n=13)				
Constant	62.5009	<0.0001	6.68759	0.0000
% organic matter	-30.9119	0.0043		
% Clay			-0.03313	0.0005
Regression		0.0043		0.0005
R-square	0.5377		0.6849	

Multiple linear regression. Table 2.2 contains the best-fit models from the stepwise multiple linear regression analysis that explored the relationship of number of taxa and number of individuals and five independent variables for each of the sampled seasons. Spatial changes in community composition are thus explained mostly by changes in sediment size, amounts of fine particles, water depth and organic matter content, the relative importance varying over the seasons. Shallower sites with coarser sediment and a low content of organic matter harbour a richer community (Figure 2.3a-f). However, the importance of each of these variables varies with season. During the northers season, the fitted model for number of families included percentage of clay and mean grain size (Table 2.2), indicating the influence of physical disturbance during the previous four months and the continuous input of fine sediment on the southern area of the shelf. After the dry and rainy seasons, however, only organic matter was included in the models (Table 2.2). This in turn could be related to the absence of the putative physical disturbance from northers and relates more to riverine deposition and quality of food. In all cases, the regression model was highly significant ($p<0.01$) and the percentage of variation explained by those variables was 72%, 39% and 53% respectively.

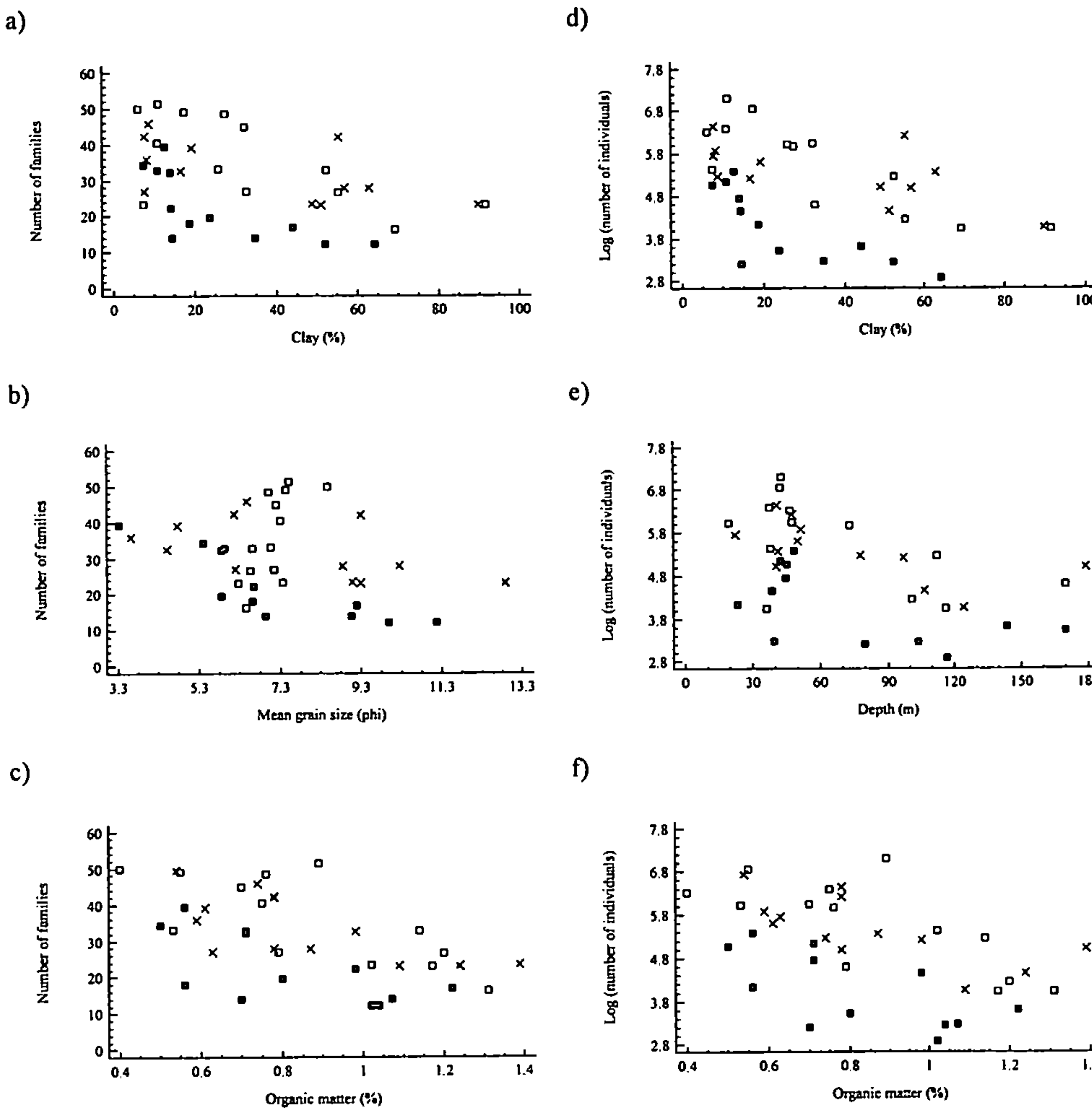


Figure 2.3. Scatter plots of the explanatory variables selected by the stepwise multiple linear regression models as shown in Table 2. Data are averages of three replicates (0.05 m^2) from each site. (◘ = northers, X = dry, □ = rainy seasons).

The fitted model for log numbers of individuals during the 'northers' season only included percentage of clay. This difference in relation to the fitted model for number of families reflects the ANOVA results (no differences in densities during 'northers') as the physical disturbance from the 'northers' drastically reduced densities all over the shelf. However, the remaining differences are best explained by the content of fine material derived from river influence. During the dry season, depth and organic matter were the best predictor variables, whilst only percentage of clay came out as the best explanatory variable during the rainy season. The percentage of variation explained by the models was 58%, 69% and 68% respectively.

Multivariate analysis.

Two-way crossed ANOSIM results for differences among seasons revealed a significant overall difference in community composition (Table 2.3), illustrated by the MDS ordination (Figure 2.4). Pairwise comparisons revealed that all possible pairs of seasons are significantly different. Similarly, all 'Blocks' were significant different from each other (Table 2.3). Seasons had variable degrees of effect on communities in different sub-environment (blocks), as observed from the MDS plot where differences between dry and rainy seasons within the blocks were comparatively slight, demonstrating an interaction effect between the two factors. Indirect formal establishment of interactions was made by one way ANOSIM of 'northers' vs. dry, 'northers' vs. rainy and dry vs. rainy, separately for each sub-environment (transitional-shallow, $R = 0.142$, $p>0.05$; carbonate-shallow, $R = 0.262$, $p<0.05$; transitional-deep $R = 0.483$, $p<0.05$, carbonate-deep $R = 0.339$, $p<0.05$). Therefore, there is no seasonal effect on the community composition in the transitional-shallow, strata most likely as a result of continuous disturbance from both rainy and 'northers' seasons.

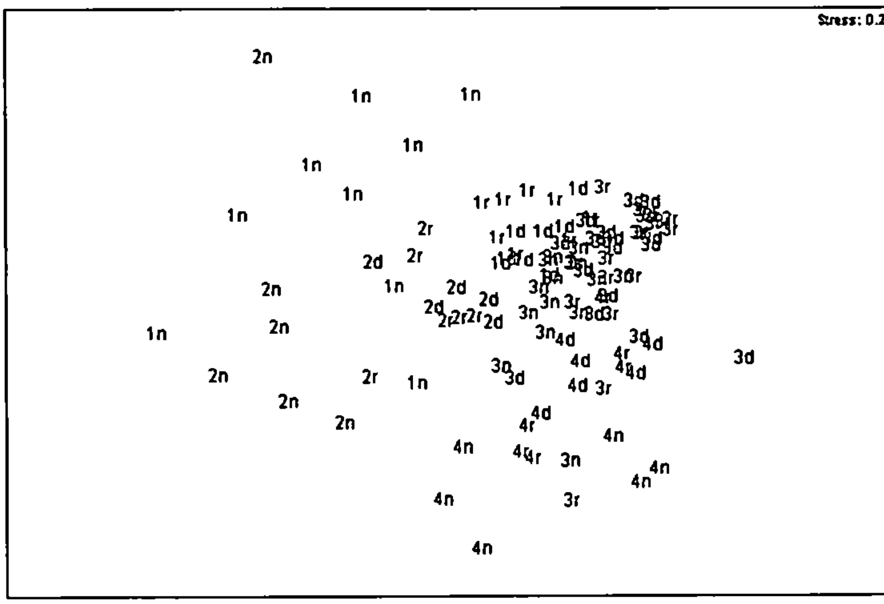


Figure 2.4. MDS ordination of the 13 replicated sites sampled on the continental shelf of the southern GoM based on fourth root transformed abundance of families and Bray-Curtis similarities. 1 = Carbonate deep, 2 = Transitional deep, 3 = Carbonate shallow, 4 = Transitional shallow. n = northers, d = dry, r = rainy seasons.

Table 2.3. Two way crossed ANOSIM testing for differences between three seasons: (northers, dry and rainy), and between four environments: carbonate-deep (CD), transitional-deep (TD), carbonate-shallow (CS) and transitional-shallow (TS). Results show rejection of the null hypothesis of no differences in community structure and composition among seasons and across sub-environments at an overall significance level of 5%.

	Global test R	Pairwise test R	Significance level (%)
Seasons	0.284		0.1
northers, dry		0.357	0.1
northers, rainy		0.445	0.1
dry, rainy		0.076	2.3
Environments	0.669		0.1
CD, TD		0.538	0.1
CD, CS		0.545	0.1
CD, TS		0.732	0.1
TD, CS		0.867	0.1
TD, TS		0.743	0.1
CS, TS		0.7	0.1

BIOENV analysis was first conducted on the overall data set and the resulting maximum correlation was 0.262 for up to two variables (depth and organic carbon). It was then undertaken independently for each season and the best results for one to three variables of the spatial analysis of relationships between community structure and a set of eight environmental variables are given in Table 2.4. For all seasons depth was the single variable best explaining community patterns.

Table 2.4. Relationship between environmental variables and fauna by season using BIOENV analysis with up to 3 environmental variables best explaining the faunal patterns. Resulting values are weighted Spearman rank correlation coefficients (r_s).

Northers		Dry		Rainy	
Variables	r_s	Variables	r_s	Variables	r_s
Depth, clay, organic matter	0.366	Depth, sorting, organic matter	**0.423**	Depth, clay, sorting	**0.580**
Depth, clay	**0.373**	Depth, sorting	0.411	Depth, clay	0.557
Depth	0.364	Depth	0.383	Depth	0.392

The families that contributed most to dissimilarities between seasons within each 'block' are given in Table 2.5a-c (SIMPER analysis). In the carbonated environment (deep and shallow) the most important families were generally the same for every pair of compared seasons, although their order of importance varied. Conversely, different important families were evident in both transitional environments for every pair of compared seasons. For example, in the transitional deep strata, variation in abundance of Sabellidae and Cossuridae contributed most to dissimilarities between 'northers' and dry season, but Ampeliscidae and Nemertea *a* were the most important for separating communities between northers and rainy season. At transitional shallow sites, polychaetes and crustaceans contributed equally to the pairwise dissimilarities, but out of these, Ampeliscidae and Lumbrineridae were particularly important between 'northers' to dry and 'northers to rainy' but did not vary so greatly from dry to rainy seasons.

Table 2.6a-d presents the SIMPER results for comparisons between 'blocks', demonstrating a shift of the discriminatory families between every pair of sub-environments within seasons and also a shift from season to season. For example, during the 'northers', polychaete, sipunculid and mollusc families discriminate between the deep environments (Table 2.6a). However, during the dry season, the main contribution to dissimilarities was from increasing numbers of polychaetes (Spionidae, Syllidae, Pilargidae and Sabellidae). After the rainy season, crustaceans (Parapseudidae and Myodocopa c) were included within the most important discriminatory families. In comparison, small changes in abundance rather than in taxon composition were the primary reason for differences between the deep and shallow carbonate environments (Table 2.6b). For example, during the 'northers', several families of polychaete worms were more abundant in shallow areas and increased their numbers from the dry to rainy seasons. In contrast in the transitional environments, both increases in abundance and changes in family composition occurred from season to season (Table 2.6c). During 'northers', Lumbrineridae, Spionidae, Ampeliscidae and Parapseudidae were very abundant in the shallow strata. Later on, during the dry season, Spionidae and Parapseudiade increased in numbers and therefore a change in composition of important families occurred from the dry to the rainy seasons. Dissimilarities between the carbonate and transitional shallow environments also related to an increase in numbers and changes in family composition (Table 2.6d).

Discussion

Spatial patterns of macroinfauna structure and composition varied across and along the Campeche Shelf as a response to sedimentary environments and depth. Coarser sediments from the carbonate area harboured the highest mean densities (500 – 24000 individuals /m^2) and number of families (108 to 122 families in total). These values are similar to the shelf environments from the north-eastern GoM where carbonate sediments have macroinfauna densities from 1280 to 14202 individuals/m^2 and species numbers >1000 (Phillips 1990). Medium to coarse sandy sediments on the inner shelf of south-east Australia can also harbour densities of macroinfauna up to 14460/m^2 and up to 700 species (Coleman *et al.* 1997). In contrast, the transitional sub-environment exhibited both low densities and number of families, relating to the amount of silt and clay associated with river runoff; silty environments from the northwestern GoM have lower densities and number of infauna species compared to coarser sediment areas (Alexander *et al.* 1981). Shelf sediments subjected to riverine discharge often have low macrofauna densities and taxa, not only due to the amount of fine material, but also related to the quantity of refractory organic matter associated with it (Rhoads *et al.* 1985, Saoyuan & Yongting 1985, Aller & Aller 1986, Alongi *et al.* 1992, Aller & Stupakoff 1996, Albertelli *et al.* 1999).

Depth also exerted a strong influence on the spatial distribution and composition of macroinfauna on the Campeche shelf. At both sedimentary environments, differences in community composition were evident between the shallow and deep shelf strata. Depth zonation in macroinfauna community structure is a widely recognised pattern on continental shelves on the GoM (Rabalais & Boesch 1987, Darnell 1990, Escobar-Briones & Soto 1997, Escobar-Briones *et al.* 1999, Rabalais *et al.* 1999), and this general pattern has been related to changes in food supply and quality, water stability and reduction of storm and wind influence (Buchanan & Moore 1986, McLusky & McIntyre 1988, Zijlstra 1988, Hyland *et al.* 1991, Danovaro & Fabiano 1997, Karakassis & Eleftheriou 1997). Although in this study the fauna was identified to family level, it was evident that the carbonate shallow shelf sub-environment is rich in taxa with high densities and that the grading into fine sedimentary and deeper environments restricts macroinfauna distribution.

Variable temporal patterns in macrobenthic community structure resulted from the strong interaction between sediment type, depth strata and processes associated with the three main climatic seasons. Out of this variability, two main patterns were clear from both the univariate and multivariate analyses. Firstly, after the 'northers' season there were low numbers of individuals and families, with no differences between sedimentary environments or depth strata and a highly variable and dissimilar community composition. The second pattern was evident during the dry and rainy seasons and represented by a general increase in both numbers of taxa and individuals, with highly significant differences between sedimentary environments and depth strata and reduced variability and dissimilarity in the community composition. However the patterns were not of the same magnitude for all the levels of the three factors considered, with changes within the carbonate environment being more marked than at transitional sites. It is therefore proposed that sediment re-working and re-suspension by physical disturbance throughout the "northers" season decreased both macroinfauna densities and families, the importance of physical variables being highlighted by regression results.

The "northers" season on the Campeche shelf is consistently linked to strong winds of 20 to 30 cm/s (Salas de Leon *et al.* 1992, Magaña *et al.* 2001), vertical mixing of the water column down to 175 m depth (Vidal *et al.* 1994) and the lowest resulting benthic biomass on the terrigenous shelf (Soto & Escobar-Briones 1995). Reduction in macroinfauna and meiofauna densities as a consequence of physical disturbance by winter storms has been documented by Dagg (1988), Thistle *et al.* (1995) and Posey *et al.* (1996) on the shallow inner shelf (<20m water depth) of the northern GoM. Similarly wave disturbance associated with winter storms on the California inner shelf is thought to be responsible for macroinfauna zonation and strong fluctuations in densities of opportunistic species (Oliver *et al.* 1980, Okey 1997). Indeed wind stress is known to limit benthic secondary production (Emerson 1989) and regulate benthic processes through disturbance of shallow shelf benthos (Alongi 1989b). Although wave disturbance associated with storms appears to be limited to shallow depths (Hall 1994)) the prevailing wave field during storms on the Campeche shelf is able to re-suspend sediment sizes from 2.5 to 6.0 mm at depths of 50 to 80 metres (Logan *et al.* 1969). In the northern GoM residual currents from winter storms can transport large amounts of sediment (in a benthic nepheloid layer) from the outer shelf (50-80m deep) towards the continental slope (McGrail & Carnes 1983).

In the absence of strong northerly winds, and the re-establishment of the general circulation pattern dominated by the Yucatan Current, a major shift in macroinfauna structure can occur, probably as a result of larval recruitment and *in situ* re-colonisation. The carbonate sub-environments were the ones where the increase was clearer and probably enhanced by the influence of shallow banks and reefs (Bogdanov *et al.* 1996). This bank and reef effect is known to influence soft bottom macroinfauna on the northern GoM (Rezak *et al.* 1990). Once the general response to the release of physical disturbance and the re-colonisation has been accomplished, there was little change measured in the studied area between dry and rainy seasons.

SIMPER analysis identified the subtle temporal changes in composition that occurred within environments between seasons. Polychaetes were the numerically dominant macrofauna taxon (Maurer & Leathem 1980, Rainer 1984, Alongi 1989b, Granados-Barba 1994). The increase in numbers of surface deposit feeder polychaetes (such as ampharetids, spionids, lumbrinerids and paraonids) from dry to rainy seasons occurred particularly within the carbonate sub-environments. This differs from the findings of Posey *et al.* (1998) namely that deposit feeders were proportionally more important during winter in the Northeast GoM; low number of spionid polychaetes have previously been reported in the area immediately after the winter (Granados-Barba & Solis-Weis 1998). Most of the polychaetes, as well as being in high numbers, were of small size which is characteristic of opportunistic fauna (Pearson & Rosenberg 1978, Yingst & Rhoads 1985, Alongi 1989a, Aller & Stupakoff 1996). Alternatively, such changes in polychaete number and size could reflect a recent recruitment event, particularly for suspension feeder polychaetes (Posey *et al.* 1998). Sabellidae, Serpulidae and Syllidae polychaetes were very abundant within the carbonate environment after the 'northers' season, the latter being known to associate with hard substrata or coarse sediment habitats (Fauchald & Jumars 1979, Uebelacker & Johnson 1984). It is therefore proposed that these families may represent the northern influence of the Yucatan current providing recent recruits to the area. Barry (1989) has reported that *Phragmatoma lapidosa californica* has a reproductive response coupled to an increase in wave disturbance.

In contrast, at the transitional environment, a combination of polychaetes, tanaids and amphipod families played a similar role in discriminating seasons, with Spionidae and Parapseudidae in particular consistently increasing in abundance from 'northers' to the dry and rainy seasons. The restrictive effect of fine sediments however, is reflected in the absence of sabellid (suspension feeder) and syllid worms (predators, deposit feeders and superficial burrowers) that were important in the carbonate and shallow sub-environment.

Similarly Flint and Rabalais (1980) have documented preferences of certain sediment types by macroinfauna in the Northern GoM.

The two analyses for linking environmental variables with the biotic patterns provide coherent results. Multivariate patterns of community composition were related to depth, sediment type/size and organic matter. These are co-variates of shelf scale processes such as fine sediment deposition from river runoff and sediment re-suspension and transport due to wave disturbance. These processes can act either at a large temporal scale or as discrete pulses (Gray 1981, Snelgrove & Butman 1994, Posey *et al.* 1996). The low correlation value (0.36) from BIOENV analysis after the 'northers' is mostly likely due to influences from unmeasured variables that mobilised sediment resulting in winnowing during autumn and winter (Wartel and Salinas, unpub. data in Fiers 1996), but did not affect patterns of sediment size. This result is consistent with the regression model that included mean grain size and percentage of clay. Therefore the low values of community measures after 'northers' appear to be related to changes in sediment composition, probably as a result of physical disturbance.

The issue of patterns and scales is considered a central problem in ecology (Milne 1991, Levin 1992) and throughout this study patterns and scales of variability in community structure driven by large scale and periodic physical processes were present over the studied period. Scales of variation from metres to tens of kilometres are recognised in soft sediment infauna (Thrush 1991, Morrisey *et al.* 1992a, Hewitt *et al.* 1998). In the southern GoM, spatial variation from replicated sites in sub-environments of "similar sedimentary conditions" truly reflected the patchy structure of infauna in continental shelves at this scale. This spatial variation is also recognised as a mechanism of increasing diversity for crustacean communities from the outer shelf to the continental slope in the terrigenous area

(Soto *et al.* 1998). The interaction of the studied factors demands generalisations of the response of infaunal communities to physical processes of large scale influences (like "northers" and river runoff on the Campeche Shelf) to be treated with caution. Strong spatial variation can affect our ability to detect any temporal variation (Morrisey *et al.* 1992b), therefore this study has a limited scope in relation to any conclusions of multi-year seasonality since no such temporal replication was applied. However it is believed that the sampling design and the spatial replication allowed for the establishment of the strong effect of depositional and depth sub-environments as well as the temporal scale of variation imposed by the "northers" season. It is considered that the recognition of these scales of variability on the Campeche Shelf are essential in order to move onto the important issue of investigating the human influence related to oil activities that have developed in the southern Gulf. A factor that has not been addressed until now and that deserves further careful consideration, is the disturbance caused by winter storms and river runoff that influence patterns on this particular shelf.

Table 2.5a. Results of SIMPER analysis indicating which families contributed most to dissimilarities between seasons, presented as average abundance (AvAb) of important macroinfauna families during the 'northers and dry season within each environment. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb Northers	AvAb Dry	AvD	AvD/SD	AvD Cum. %
Carbonate deep. Total average dissimilarity = 69.19					
Spionidae	1.44	21.38	6.08	1.14	8.79
Syllidae	0.67	19	4.12	1.48	14.75
Tellinidae	2.44	2.25	3.73	1.46	20.14
Aspidosiphonidae	3.22	4.25	3.53	1.45	25.25
Onuphidae	2.78	6.88	3.14	1.31	29.79
Ampharetidae	0.56	13.38	3.07	1.97	34.23
Sabellidae	0.44	10.75	2.96	1.49	38.51
Maldanidae	2.56	6.38	2.34	1.48	41.9
Paraonidae	0.89	9.5	2.27	1.66	45.18
Cirratulidae	1.33	5	2.23	1.06	48.4
Pilargidae	1.67	10.88	1.97	1.06	51.24
Transitional deep Total Average Dissimilarity = 67.52					
Cirratulidae	4.33	9.6	5.08	1.29	7.53
Aspidosiphonidae	1.67	5.2	4.03	1.89	13.5
Dentalidae	1.67	0	3.64	0.98	18.89
Spionidae	0.67	5.8	3.6	1.37	24.22
Nephtyidae	2	3.6	2.77	1.39	28.32
Trichobranchidae	0.67	2.8	2.7	1.23	32.31
Ampharetidae	0	3.6	2.62	2.76	36.2
Maldanidae	1.17	1.8	2.6	1.41	40.05
Paraonidae	0	3.6	2.4	2.05	43.6
Sabellidae	0.33	2.2	2.12	1.47	46.74
Chaetopteridae	0.33	1.8	1.86	0.95	49.5
Cossuridae	0.33	2.2	1.81	1.02	52.19
Carbonate shallow Total Average Dissimilarity = 54.92					
Spionidae	17.8	103.44	5.4	1.52	9.83
Paraonidae	9.27	49.11	4.2	1.22	17.48
Syllidae	6.33	45.44	3.86	1.12	24.52
Sabellidae	15.07	52.33	3.58	1.33	31.03
Lumbrineridae	16.07	27.78	3.57	1.45	37.53
Cirratulidae	6.8	7.06	1.98	1.04	41.14
Aspidosiphonidae	5.93	3.5	1.79	0.95	44.39
Lineidae	5.8	13.78	1.45	1.23	47.04
Capitellidae	5.4	10.83	1.34	0.74	49.49
Parapseudidae	0.8	7.11	1.34	0.49	51.93
Transitional shallow Total Average Dissimilarity = 61.87					
Spionidae	5.83	78.33	9.82	2.14	15.88
Lumbrineridae	8.17	13.83	5.26	1.26	24.38
Ampeliscidae	6	5.5	4.76	1.23	32.07
Capitellidae	1	32.67	4.49	1.74	39.33
Parapseudidae	3.33	25.17	4.09	1.16	45.94
Nanastacidae	1.17	8.83	2.96	1.14	50.72

Table 2.5b. Results of SIMPER analysis indicating which families contributed most to dissimilarities between seasons, presented as average abundance (AvAb) of important macroinfauna families during 'northers' and rainy seasons within each environment. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb Northers	AvAb Rainy	AvD	AvD/SD	AvD Cum. %
Carbonate deep. Total average dissimilarity = 71.8					
Aspidosiphonidae	3.22	15.67	5.16	1.32	7.18
Syllidae	0.67	30.33	5.13	1.37	14.33
Spionidae	1.44	17.56	4.57	1.27	20.69
Tellinidae	2.44	1.33	4.1	1.62	26.41
Onuphidae	2.78	4.33	3.15	1.25	30.79
Cirratulidae	1.33	11.56	2.79	1.11	34.67
Maldanidae	2.56	6.11	2.56	1.44	38.25
Sabellidae	0.44	10.56	2.43	1.21	41.63
Paraonidae	0.89	11.89	2.36	1.55	44.92
Ampharetidae	0.56	11.22	2.21	1.46	48
Pilargidae	1.67	9	2.07	1.24	50.89
Transitional deep. Total Average Dissimilarity = 69.38					
Parapseudidae	0.17	6.67	5.11	1.73	7.36
Cirratulidae	4.33	6.83	4.98	1.4	14.54
Aspidosiphonidae	1.67	4.83	3.97	1.36	20.26
Dentalidae	1.67	0.5	3.48	1.01	25.28
Nephtyidae	2	2.83	2.84	1.76	29.37
Spionidae	0.67	4.17	2.57	1.99	33.07
Maldanidae	1.17	1.33	2.4	1.52	36.53
Paraonidae	0	2.67	2.34	1.27	39.9
MYODOCOPA C	0	2.83	2.16	2.03	43.02
Ampeliscidae	0	2.5	2.11	1.84	46.06
NEMERTEA A	0.5	1.17	1.85	0.79	48.73
Onuphidae	1.17	5	1.73	1.25	51.23
Carbonate shallow. Total Average Dissimilarity = 57.28					
Paraonidae	9.27	74.94	5.67	0.85	9.9
Sabellidae	15.07	117.76	5.22	1.38	19.01
Spionidae	17.8	94.76	4.48	1.12	26.83
Lumbrineridae	16.07	39.59	4.43	1.32	34.56
Syllidae	6.33	63	2.74	1.41	39.34
Cirratulidae	6.8	9.29	2.02	1.07	42.88
Aspidosiphonidae	5.93	3.24	1.91	0.99	46.21
Nereididae	1.2	31.94	1.72	1.1	49.22
Lineidae	5.8	9.41	1.35	1.31	51.59
Transitional shallow. Total Average Dissimilarity = 64.65					
Parapseudidae	3.33	71	8.7	1.2	13.45
Lumbrineridae	8.17	8.5	6.03	1.31	22.78
Spionidae	5.83	23.5	5.69	1.51	31.58
Ampeliscidae	6	5.67	4.37	1.18	38.34
Nephtyidae	1	4.5	3.08	1.35	43.1
Nanastacidae	1.17	2	2.66	1.13	47.21
Capitellidae	1	24.17	2.39	1.01	50.91

Table 2.5c. Results of SIMPER analysis indicating which families contributed most to dissimilarities between seasons, presented as average abundance (AvAb) of important macroinfauna families during dry and rainy seasons within each environment. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb Dry	AvAb Rainy	AvD	AvD/SD	AvD Cum. %
Carbonate deep. Total average dissimilarity = 50.38					
Spionidae	21.38	17.56	5.48	1.22	10.87
Syllidae	19	30.33	3.97	1.44	18.75
Aspidosiphonidae	4.25	15.67	3.66	0.67	26.02
Sabellidae	10.75	10.56	1.96	1.33	29.91
Onuphidae	6.88	4.33	1.84	1.2	33.56
Pilargidae	10.88	9	1.82	1.23	37.17
Ampharetidae	13.38	11.22	1.73	1.17	40.61
Cirratulidae	5	11.56	1.71	0.72	44.02
Paraonidae	9.5	11.89	1.45	1.21	46.89
Serpulidae	0.38	10.11	1.23	0.48	49.33
Terebellidae	4.5	1.78	1.18	1.44	51.66
Transitional deep. Total Average Dissimilarity = 55.54					
Parapseudidae	1	6.67	4.79	1.62	8.62
Cirratulidae	9.6	6.83	3.26	2.28	14.49
Trichobranchidae	2.8	0	2.69	0.93	19.34
Aspidosiphonidae	5.2	4.83	2.48	1.71	23.8
Spionidae	5.8	4.17	2.43	1.26	28.18
MYODOCOPA C	0	2.83	2.16	2.03	32.08
Onuphidae	3.6	5	1.87	1.36	35.44
Chaetopteridae	1.8	0.83	1.79	0.92	38.66
Paraonidae	3.6	2.67	1.77	1.44	41.85
Maldanidae	1.8	1.33	1.75	1	45.01
Ampharetidae	3.6	1.17	1.67	1.46	48.02
Nephtyidae	3.6	2.83	1.61	1.58	50.91
Carbonate shallow. Total Average Dissimilarity = 50.7					
Paraonidae	49.11	74.94	6.61	1.11	13.03
Spionidae	103.44	94.76	5.29	1.54	23.46
Sabellidae	52.33	117.76	4.95	1.33	33.22
Syllidae	45.44	63	3.58	1.16	40.27
Lumbrineridae	27.78	39.59	3.35	0.83	46.88
Parapseudidae	7.11	9.88	1.81	0.64	50.45
Transitional shallow. Total Average Dissimilarity =52.08					
Spionidae	78.33	23.5	9.13	1.58	17.53
Parapseudidae	25.17	71	8.62	1.31	34.09
Capitellidae	32.67	24.17	3.3	1.34	40.42
Nanastacidae	8.83	2	3.02	1.18	46.21
Nephtyidae	3.17	4.5	2.97	1.21	51.92

Table 2.6a. Results of SIMPER analysis indicating which families contributed most to dissimilarities between environments, presented as average abundance (AvAb) of important macroinfauna families at the carbonate and transitional deep environments within each season. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb CD	AvAb TD	AvD	AvD/SD	AvD Cum. %
After Northers Season. Total average dissimilarity = 71.78					
Cirratulidae	1.33	4.33	6.84	1.42	9.53
Aspidosiphonidae	3.22	1.67	4.29	1.56	15.51
Nephtyidae	0.56	2	3.8	1.66	20.81
Tellinidae	2.44	0.5	3.7	1.44	25.96
Dentalidae	0.22	1.67	3.54	1	30.9
Onuphidae	2.78	1.17	2.94	1.38	35
Maldanidae	2.56	1.17	2.55	1.34	38.56
Spionidae	1.44	0.67	2.08	1.04	41.45
Sigalionidae	0.78	0.5	2.07	0.99	44.33
Pilargidae	1.67	0.83	2.03	1.19	47.17
Lucinidae	0.44	0.67	1.98	0.76	49.93
Sabellidae	0.44	0.33	1.91	0.66	52.59
After Dry Season. Total Average Dissimilarity = 58.88					
Spionidae	21.38	5.8	5.4	1.2	9.18
Cirratulidae	5	9.6	4.86	1.46	17.43
Syllidae	19	2.4	3.35	1.27	23.13
Aspidosiphonidae	4.25	5.2	2.78	1.56	27.85
Trichobranchidae	0.75	2.8	2.66	0.96	32.37
Pilargidae	10.88	0.4	2.64	1.58	36.84
Onuphidae	6.88	3.6	1.98	1.36	40.2
Nephtyidae	3.25	3.6	1.93	1.37	43.48
Maldanidae	6.38	1.8	1.92	1.42	46.75
Sabellidae	10.75	2.2	1.86	1.24	49.9
Chaetopteridae	0.5	1.8	1.75	0.81	52.88
After Rainy Season. Total Average Dissimilarity = 65.32					
Parapseudidae	2.67	6.67	5.2	1.85	7.96
Syllidae	30.33	1.17	5.19	1.33	15.91
Aspidosiphonidae	15.67	4.83	4.83	1.16	23.3
Spionidae	17.56	4.17	3.47	1.07	28.62
Cirratulidae	11.56	6.83	3.44	2.54	33.88
Onuphidae	4.33	5	2.4	1.73	37.56
Pilargidae	9	0.33	2.32	1.37	41.11
Myodocopa C	2.22	2.83	1.91	1.76	44.04
Ampharetidae	11.22	1.17	1.91	1.6	46.97
Nephtyidae	2.56	2.83	1.83	1.91	49.78
Paraonidae	11.89	2.67	1.79	1.19	52.51

Table 2.6b. Results of SIMPER analysis indicating which families contributed most to dissimilarities between environments, presented as average abundance (AvAb) of important macroinfauna families at the carbonate deep and shallow environments within each season. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

	AvAb	AvAb	AvD	AvD/SD	AvD Cum.
Families	**CD**	**CS**			**%**
After Northers Season. Total average dissimilarity = 73.12					
Spionidae	1.44	17.8	5.37	1.18	7.34
Lumbrineridae	0.56	16.07	5.22	1.88	14.48
Sabellidae	0.44	15.07	4.09	1.28	20.08
Tellinidae	2.44	1.67	3.93	1.57	25.45
Aspidosiphonidae	3.22	5.93	3.39	1.47	30.09
Onuphidae	2.78	4.67	3.3	1.27	34.61
Maldanidae	2.56	3.8	2.67	1.42	38.26
Cirratulidae	1.33	6.8	2.65	1.24	41.89
Paraonidae	0.89	9.27	2.54	1.74	45.36
Syllidae	0.67	6.33	2.1	1.11	48.23
Pilargidae	1.67	1.73	1.95	1.05	50.9
After Dry Season. Total Average Dissimilarity = 56.07					
Spionidae	21.38	103.44	6.3	1.65	11.24
Paraonidae	9.5	49.11	4.3	1.17	18.91
Syllidae	19	45.44	3.47	1.24	25.11
Sabellidae	10.75	52.33	3.08	1.39	30.6
Ampharetidae	13.38	6.39	2.97	2.17	35.9
Pilargidae	10.88	6.44	2.24	1.36	39.89
Lumbrineridae	2.88	27.78	2.16	1.36	43.74
Onuphidae	6.88	3.28	2	1.08	47.32
Maldanidae	6.38	5.44	1.49	1.85	49.98
Nereididae	0.75	17.22	1.44	1.42	52.54
After Rainy Season. Total Average Dissimilarity = 63.89					
Paraonidae	11.89	74.94	5.87	0.87	9.19
Sabellidae	10.56	117.76	5.83	1.44	18.32
Spionidae	17.56	94.76	4.68	1.29	25.64
Syllidae	30.33	63	4.2	1.34	32.22
Aspidosiphonidae	15.67	3.24	3.81	0.65	38.17
Lumbrineridae	3.78	39.59	3.79	0.81	44.11
Pilargidae	9	4.12	2.29	1.36	47.7
Ampharetidae	11.22	7.41	2.11	1.55	51

Table 2.6c. Results of SIMPER analysis indicating which families contributed most to dissimilarities between environments, presented as average abundance (AvAb) of important macroinfauna families at the Transitional deep and shallow environments within each season. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb TD	AvAb TS	AvD	AvD/SD	AvD Cum. %
After Northers Season. Total average dissimilarity = 83.19					
Lumbrineridae	0.17	8.17	7.34	1.55	8.82
Cirratulidae	4.33	1.17	7.1	1.47	17.36
Spionidae	0.67	5.83	5.63	2.58	24.13
Ampeliscidae	0	6	5.4	1.26	30.61
Aspidosiphonidae	1.67	1	3.92	1.05	35.33
Dentalidae	1.67	0	3.64	0.99	39.7
Nephtyidae	2	1	3.25	1.4	43.61
Parapseudidae	0.17	3.33	3.07	0.99	47.3
Maldanidae	1.17	0.17	2.68	1.32	50.52
After Dry Season. Total Average Dissimilarity = 71					
Spionidae	5.8	78.33	12.41	2.39	17.48
Cirratulidae	9.6	3.17	5.4	1.58	25.08
Capitellidae	2.2	32.67	4.48	1.64	31.39
Parapseudidae	1	25.17	4.17	1.08	37.27
Aspidosiphonidae	5.2	2.5	3.48	2.18	42.17
Nanastacidae	0.4	8.83	2.91	1.07	46.26
Trichobranchidae	2.8	0	2.69	0.93	50.05
After Rainy Season. Total Average Dissimilarity = 69.34					
Parapseudidae	6.67	71	8.5	1.57	12.26
Spionidae	4.17	23.5	6.33	1.07	21.4
Cirratulidae	6.83	4.67	3.74	2.86	26.79
Onuphidae	5	0.5	3.56	3.05	31.92
Capitellidae	0.33	24.17	3.26	1.33	36.61
Aspidosiphonidae	4.83	2.5	3.19	1.58	41.22
Nephtyidae	2.83	4.5	2.96	2.14	45.49
Paraonidae	2.67	7.83	2.21	1.23	48.67
Myodocopa C	2.83	0	2.16	2.03	51.79

Table 2.6d. Results of SIMPER analysis indicating which families contributed most to dissimilarities between environments, presented as average abundance (AvAb) of important macroinfauna families at the Carbonate and Transitional shallow environments within each season. The AvD/SD ratio measures how consistently a family contributed towards the average dissimilarity (AvD).

Families	AvAb CS	AvAb TS	AvD	AvD/SD	AvD Cum. %
After Northers Season. Total average dissimilarity = 65.01					
Ampeliscidae	0.47	6	5.28	1.26	8.13
Lumbrineridae	16.07	8.17	4.53	1.35	15.1
Sabellidae	15.07	0	4.21	1.25	21.58
Spionidae	17.8	5.83	3.25	1.02	26.57
Parapseudidae	0.8	3.33	2.99	0.93	31.17
Paraonidae	9.27	0.67	2.45	1.61	34.93
Cirratulidae	6.8	1.17	2.37	1.31	38.58
Nanastacidae	1	1.17	2.36	1.02	42.21
Lineidae	5.8	1	2.04	1.45	45.35
Onuphidae	4.67	0.83	1.94	1.09	48.33
Syllidae	6.33	0	1.86	1.55	51.19
After Dry Season. Total Average Dissimilarity = 59.14					
Spionidae	103.44	78.33	7.33	1.59	12.39
Syllidae	45.44	0	5.34	1.46	21.42
Capitellidae	10.83	32.67	4.58	1.87	29.16
Parapseudidae	7.11	25.17	4.52	1.16	36.8
Sabellidae	52.33	0	4.32	1.45	44.1
Paraonidae	49.11	11.67	4.22	1.17	51.24
After Rainy Season. Total Average Dissimilarity =68.04					
Parapseudidae	9.88	71	8.9	1.06	13.07
Sabellidae	117.76	8.5	6.34	1.4	22.39
Spionidae	94.76	23.5	6.16	1.3	31.44
Paraonidae	74.94	7.83	6.15	0.91	40.48
Syllidae	63	0.67	3.51	1.43	45.64
Lumbrineridae	39.59	8.5	3.18	0.72	50.32

CHAPTER 3

ASSESSING THE IMPACT OF NATURAL DISTURBANCE ON THE BENTHIC MACROINFAUNA OF THE CAMPECHE BANK

Introduction

Disturbance influences marine soft bottom macroinfauna assemblages by opening space (through for example migration, mortality and loss of rare species), causing changes in diversity, and generally a low biomass and relatively low productivity (Thistle 1981, Probert 1984, Emerson 1989, Hall *et al.* 1994, Kaiser 2000). Disturbance creates a mosaic of patches accompanied by macrobenthic succession along disturbance gradients they are also associated changes in dominance structure caused by increasing densities of small deposit feeding macroinfauna (Pearson & Rosenberg 1987, Reise 1991, Hall 1994, Warwick & Clarke 1994, Ellis *et al.* 2000). Tropical shelf environments are typically influenced by large-scale physical disturbance such as storms, intensive river runoff, and global climatic phenomena e.g. ENSO (Murray *et al.* 1982, Alongi 1989b, 1990, Mills *et al.* 1996, Lizano 1998). Their combined action strongly structures macrobenthic communities along depth and sedimentary gradients associated with erosion/deposition, hypoxia-anoxia events, changes in water column stability and food supply (Rhoads *et al.* 1985, Aller & Aller 1986, Garcia & Salzwedel 1991, Harper *et al.* 1991, Alongi *et al.* 1992). The spatial and temporal macrobenthic response usually follows Pearson and Rosenberg's, (1978) general model of organic enrichment, i.e. severe mortality and fauna impoverishment with subsequent "recovery" by a large influx of opportunistic species.

Identifying the response of macrobenthic assemblages to various disturbances acting concomitantly, and at various spatial and temporal scales, is difficult and requires adequate representation of the scales at which disturbance is working (Barry & Dayton 1991, Beukema *et al.* 1996, Hewitt *et al.* 1998, Zajac *et al.* 1998, Thrush *et al.* 1999, Zajac 1999). The Southern GoM combines river runoff influence, winter storms and a gradational sedimentary environment of terrigenous and carbonate sediments (Bello & Cano 1991, Aguayo-Camargo *et al.* 1999, Fuentes-Yaco *et al.* 2001). This physical setting produces a heterogeneous benthic habitat where temporal and spatial patterns of macroinfaunal assemblages are contingent on the prevailing hydrodynamic regime and sedimentary environment (see Chapter 2). In addition to this natural temporal and spatial variability, the presence of an extensive area of offshore oil production potentially contributes to changes in the structure of benthic communities.

Ecological research in the Southern GoM has emphasised that winter storms and river runoff are the most important physical processes influencing benthic community structure, function and interactions across and along the carbonate and terrigenous shelves (Yañez-Arancibia & Sanchez-Gil 1983, Soto & Escobar-Briones 1995, Fuentes-Yaco *et al.* 2001). Further work is still required, however, in relation to smaller scales of spatial variation (tens of kilometres) and temporal changes, particularly in the area of offshore oil activities, in order to gather relevant information to differentiate between natural and anthropogenic disturbance. The aim of this chapter therefore is to identify and describe spatial and temporal patterns of the macrobenthic community structure within the oil exclusion area of the Southern GoM. i.e at a smaller spatial scale than previous work and in relation to its proximity with river influence and temporal changes that may occur due to varying conditions associated with the rainy and "northers" seasons. Specifically to test the hypothesis of no differences in community structure after the putative disturbance produced by the rainy and 'northers' season within a relatively homogenous sedimentary environment

Methods

Study site

The study location covers the area between 19° 00' to 19° 40' latitude North and 91° 40' to 92° 30' longitude West, within the muddy transitional environment of the carbonate and terrigenous provinces of the Campeche Bank and Bay. Sediment size here ranges from very fine sands, through silts to clay, with a gradient of sedimentation with depth. Its carbonate content varies between 25 to 75% and bulk organic matter is high (above 2-5%) compared to the northern carbonate shelf, mainly as a result of river deposition (Hedges & Parker 1976, Gutierrez-Estrada & Galaviz-Solis 1991, Carranza-Edwards *et al.* 1993). Discharges from the Grijalva-Usumacinta and San Pedro-San Pablo rivers (Figure 3.1), winter storms or "Northers" and intrusion of oceanic water from the Caribbean current (Figure 1.4) are the driving physical processes on the shelf (Monreal-Gomez *et al.* 1992, Salas-de-Leon *et al.* 1992, Vidal *et al.* 1994). The water circulation pattern is driven by the Caribbean current during the spring and summer, with a south to south-west direction, but during autumn and winter the flow reverts to an east to north-east direction (Boicourt *et al.* 1998, Martinez-Lopez & Pares-Sierra 1998, Vidal-Lorandi *et al.* 1999). Water column stability changes from stratified to homogenous between the rainy and the 'northers' seasons, markedly affecting the inner shelf (<30m depth) (Czitrom *et al.* 1986). The study area represents the largest offshore oil production region in Mexico, with an area of 8000 km^2 and more than 200 platforms covering a range of activities (PEMEX 2001).

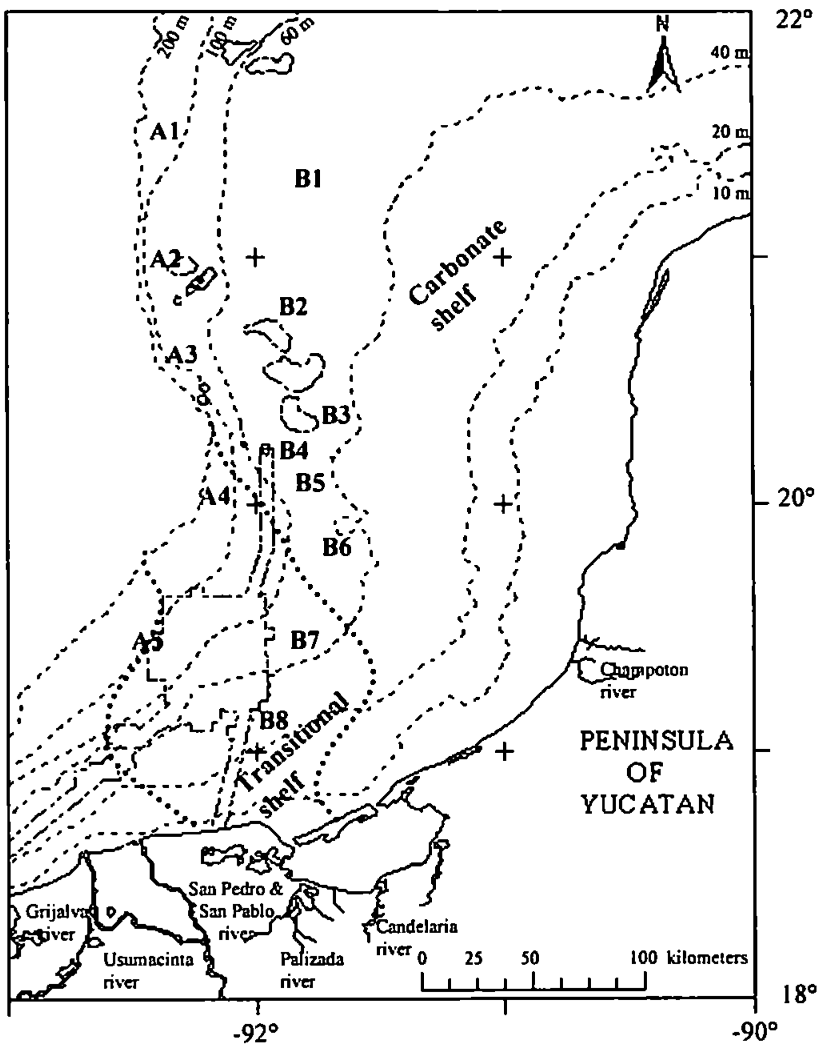


Figure 3.1. The southern Gulf of Mexico showing the carbonate and transitional sedimentary provinces and the offshore oil-activities zone at the spatial scale described in chapter 2.

Study design

The sampling design consisted of four transects (Figure 3.2). Transects A & B started 40 km NW offshore of the Terminos Lagoon system and extended to approximately 80km offshore, consequently, they followed a depth gradient of 12 to 135 metres and a sediment gradient of coarse silt to clay. Transect C & D followed a putative sediment and carbonate content gradient from fine to coarse, whilst depth was kept relatively constant, ranging from 30 to 50 metres (with the exception of stations D1 and D2 at 67m depth). These transects commenced 60-70 km NNE offshore from the rivers' mouths and extended to approximately 80km along-shore. Twelve sites were allocated to each transect approximately 7-8 km apart. The number of allocated sites was restricted by the available budget and ship time, although the chosen distance between stations was considered to represent the scale of variation likely to exist based on previous experience of the area (Chapter 2). Additionally, each pair of transects transversed the offshore oil-activities zone, increasing the number of sampled stations at the intersection point of the transects (Figure 3.2). This design incorporates the main putative gradients of river and winter storm influence by following changes in depth, sediment size and carbonate content.

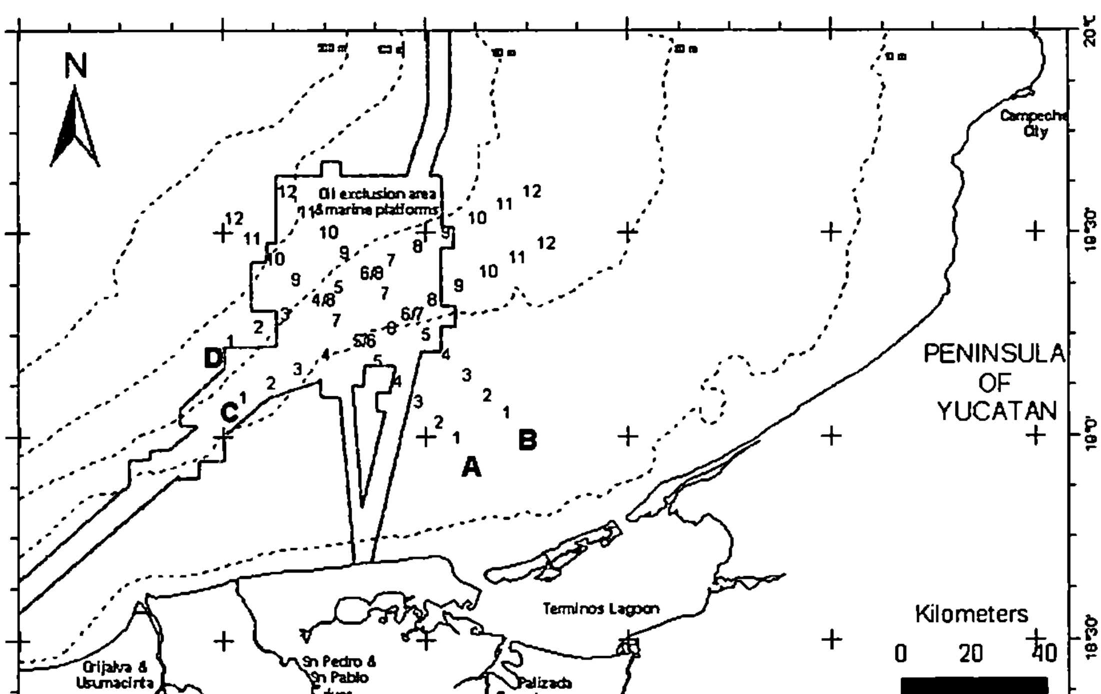


Figure 3.2. Area of study showing the stations' location along the four transects A-D. Stations were sampled for superficial sediments in November 1999 after the rainy season and April 2000 after the 'northers' season. Transects A-B followed a depth gradient and C-D followed a putative sediment gradient. (N.B. compare the spatial scales and sampling density with Figure 3.1).

Sampling methodology

Sampling was carried out from 11th - 13th November 1999 after the rainy season and from 14th – 16th April 2000 after the 'northers' season and at the beginning of the dry season. Stations were located and positioned using the satellite navigation system of the vessel and sampled without replication (using a box corer) in order to cover a larger area. Additional information recorded included depth and bottom salinity from each station (Appendix 3a-b and 4a-b). The recovered core was sub-sampled for organic matter, carbonate content and grain size analysis. Samples were taken using a PVC core of 10 cm in diameter to a depth of 5 cm, transferred to a plastic bag previously labelled and frozen until analysis. Two fractions of macroinfauna were sampled from each site. Small macroinfauna was sampled using a sub-core of 0.01 m^2 x 20 cm depth and sieved through a 0.5 mm mesh. Large macroinfauna was recovered from the remaining sediment after removing all the above samples and sieved through a 2.0 mm mesh. Sample size was 0.14 m^2 and 0.23 m^2 for November and April respectively and this was due to different box corers being available on each cruise. Samples were fixed in 5% formaldehyde solution buffered in seawater and stained with Rose Bengal prior to initial storage.

Laboratory analyses

Macroinfauna samples were transferred to a solution of 70% ethanol. Organisms were sorted, counted, wet weighed and identified to family level using taxonomic literature available for the GoM (Uebelacker & Johnson 1984, Williams 1984, Kensley & Schotte 1989, Granados-Barba 1994) and from other areas (Lincoln 1979, Holdich & Jones 1983, Barnard & Karaman 1991). Identification of the fauna to family level has been proved to be sufficient for environmental impact studies in the southern GoM (Hernandez-Arana

1995) and other areas (Long & Lewis 1987, Ferraro & Cole 1992, Somerfield & Clarke 1995). Organic matter content of sediment was measured using the ignition technique (Dean 1974). Carbonate content was analysed by acid digestion and titration. Grain size distributions were measured with a Malvern Mastersizer X laser particle sizer (Wolfe & Michibayashi 1995) and descriptive statistics (mean, sorting or inclusive standard deviation) calculated in phi units using the moment measure approach. Additional data included the specific surface area of the sediments and the percentage of sand, silt and clay.

Data analyses

Univariate approach. Simple graphs of selected environmental variables and biological measures (number of families and individuals, biomass and Shannon-Wiener diversity index Log_e) were plotted along transects for each fraction/season in order to identify spatial patterns of distribution.

Stepwise multiple linear regression analysis was undertaken to explore the relationship between depth, mean grain size (MGS, phi units), percentage of silt, sorting of sediment and percentage of organic matter using number of individuals, number of taxa and biomass. The aim was to investigate which variables best explained the univariate patterns observed for each faunal size/season. All community measures were tested for departures from normality using Wilks λ test and log-transformed when necessary (number of individuals and biomass only).

Multivariate approach. Multivariate analysis was undertaken by utilising the PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 software package (See Clarke & Warwick 1994, Clarke & Gorley 2001 for details). The two sets of 10 environmental variables from each fraction/season were subjected to Principal Component Analysis (PCA) on a normalised correlation matrix after suitable transformation (arcsin transformation for variables expressed as percentages (Sokal & Rohlf 1995) and Log_{10} for the remaining variables except depth).

For analysis of faunal patterns, non-metric multidimensional scaling (nMDS) ordination plots were produced using a ranked similarity matrix, based on Bray-Curtis similarity measures of fourth root transformed macroinfauna family abundance and biomass data for each fraction/season. Formal tests of differences in community composition between seasons for each fraction were performed by means of one-way ANOSIM (Clarke & Green 1988, Clarke 1993) on the abundance and biomass similarity matrices.

The relationship between community structure and environmental variables was explored by superimposition of selected environmental variables on abundance ordination plots and, more objectively, by the BIOENV procedure (Clarke & Ainsworth 1993). BIOENV uses a Spearman's Rank Correlation between the resulting ranked similarity matrices of fauna and correlation-based PCA of the normalised environmental variables. Variables were checked for co-correlation and those with Pearson Product Moment coefficients of 0.95 or higher were removed; hence the analysis was run on the same set of five variables used for the multiple linear regression analysis. Finally, families contributing most to any dissimilarities between seasons were investigated by the similarities percentages procedure SIMPER (Clarke 1993).

Results

Appendices 3a-b, 4a-b and 5a-b contain a summary of data of sediment variables, abundance, biomass, number of families and diversity (H'*e*) for each station and season.

Univariate analysis

Patterns of environmental variables along transects.

Transects A-B presented the major spatial changes in the measured natural variables (Figure 3.3). Stations < 30m depth had a sediment MGS within the very coarse to coarse silt on Friedman and Sanders (1978) scale, carbonate content > 50% and bulk organic matter below 6% without temporal differences between seasons. Bottom salinity, however, exhibited a temporal difference as a result of river runoff, and oceanic water intrusion during the rainy to winter-dry period of 99-00. Stations deeper than 30m had a much smaller, or even negligible change both spatially and temporally and were similar to stations along transects C-D (Figure 3.3) where sediment MGS was within the range of medium to fine silt. Carbonate content tended to increase from SW to SE and was higher along transect C. Bulk organic matter varied from 5 to 17% with some peaks along transect D but no clear gradient, and bottom salinity had only a small temporal difference in the centre of transect C.

Patterns of biological variables along transects

Small macroinfauna. In general, all biological measures increased at most sites from November to April (Figure 3.4). Along transects A-B, all biological measures had high values at stations 1 to 5 (<30m deep) with low variability, but decreased at stations 6-9 except for station B8 in April that presented the highest number of taxa and individuals. Generally, outer shelf stations were impoverished but variability among these sites (6 to

12) was high compared with sites <30m deep. Along transects C-D, however, there was no clear spatial pattern, although transect C had lower values for all biological variables than D in both seasons. Stations 5-9 in transect D demonstrated the highest variability (Figure 3.4).

Large macroinfauna. Unfortunately, number of taxa and diversity are not comparable temporally due to the difference in sample size. However, densities expressed per m^2 suggest an increase from November to April (figure 3.5). Along transect A and B, stations 1 to 5 (<30m deep) have the highest values for all biological measures except diversity in April. In November an abrupt decrease was observed either at A5/A6 and B5/B6, and comparatively low values were maintained throughout the rest of the stations into deeper waters. Number of taxa and individuals were consistently low and invariable throughout transects C and D in both seasons, with remarkably little change in density. The most impoverished sites were C5, D4 and D7 (the latter without infauna) in November, but in April were C3 and D9. Biomass and diversity presented a comparatively erratic pattern tending to stabilise towards the SE extreme of the transects (figure 3.5).

Multiple linear regression analysis

Table 3.1 presents the best-fit models (statistically significant at $p<0.05$) to explain the variation in number of taxa, $\log_{10}$ number of individuals and $\log_{10}$ biomass in terms of $\log_{10}$ (depth m), arcsin (% organic matter/100), arcsin (% silt/100), mean grain size (phi) and sorting of sediment.

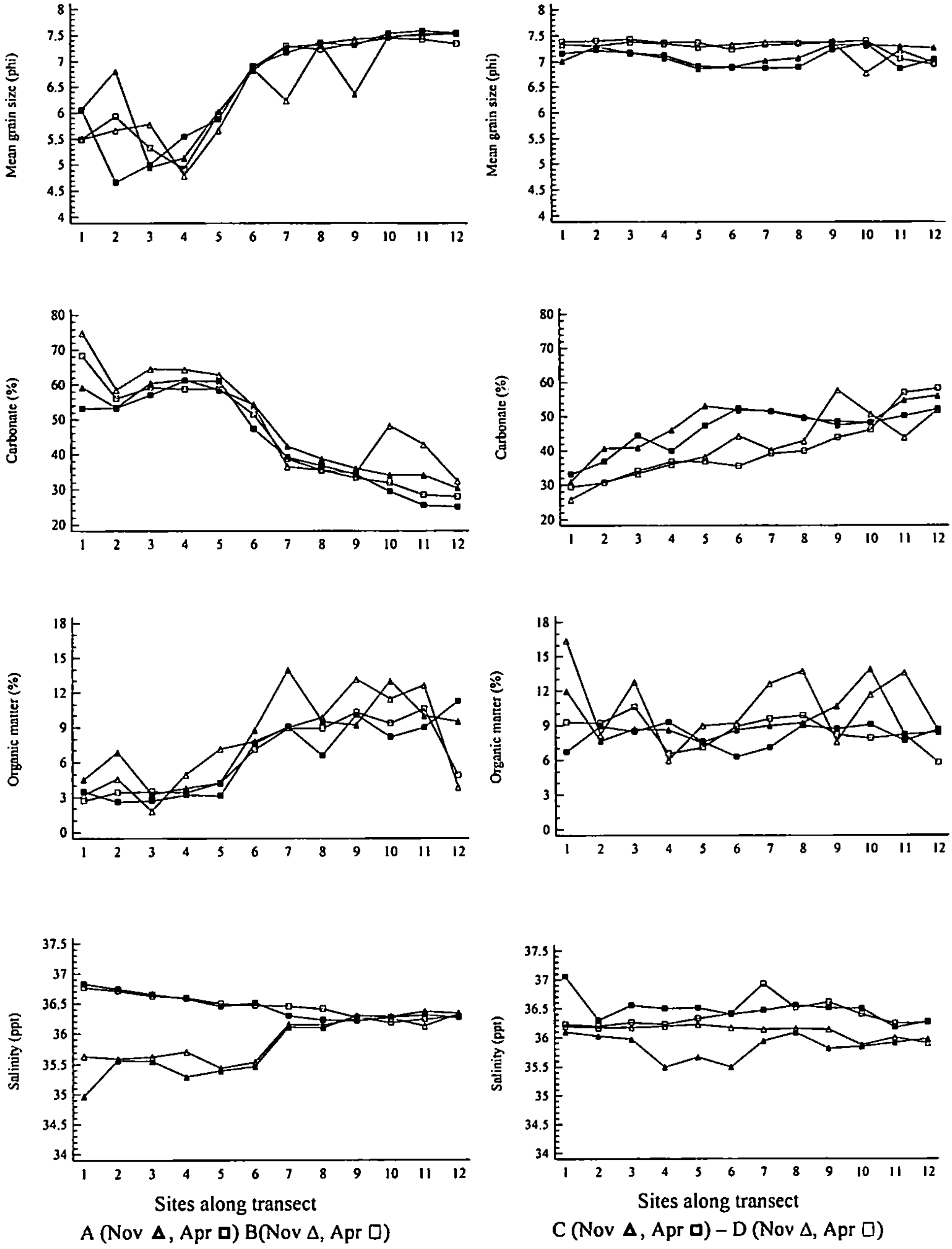


Figure 3.3. Patterns of natural environmental variables measured at each site along transects A to D. Lines are as an aid to follow the transect.

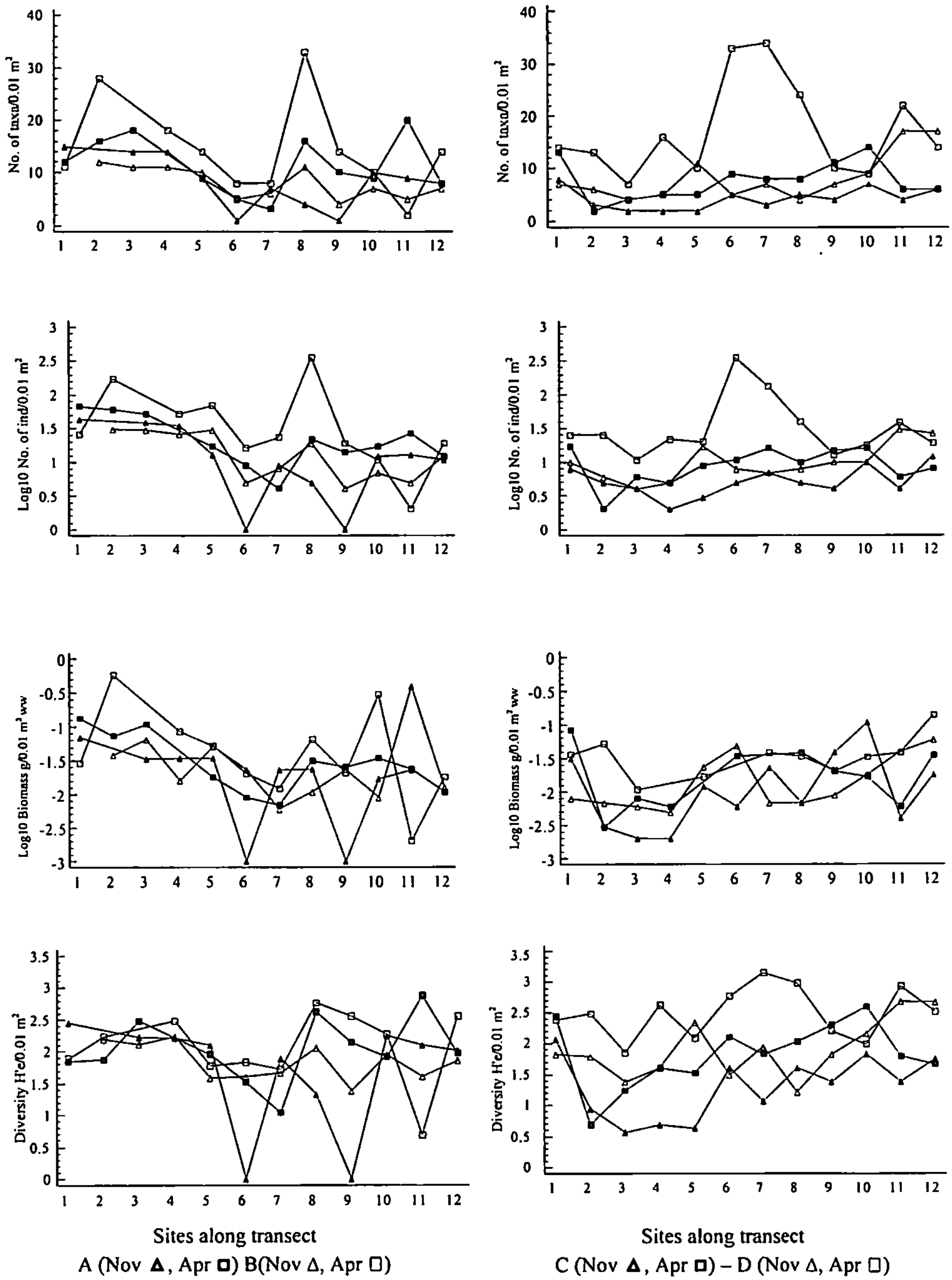


Figure 3.4. Small macrofauna patterns of biological measures at each station along transects A to D. Lines are as an aid to follow the transect. Biomass is wet weight (ww).

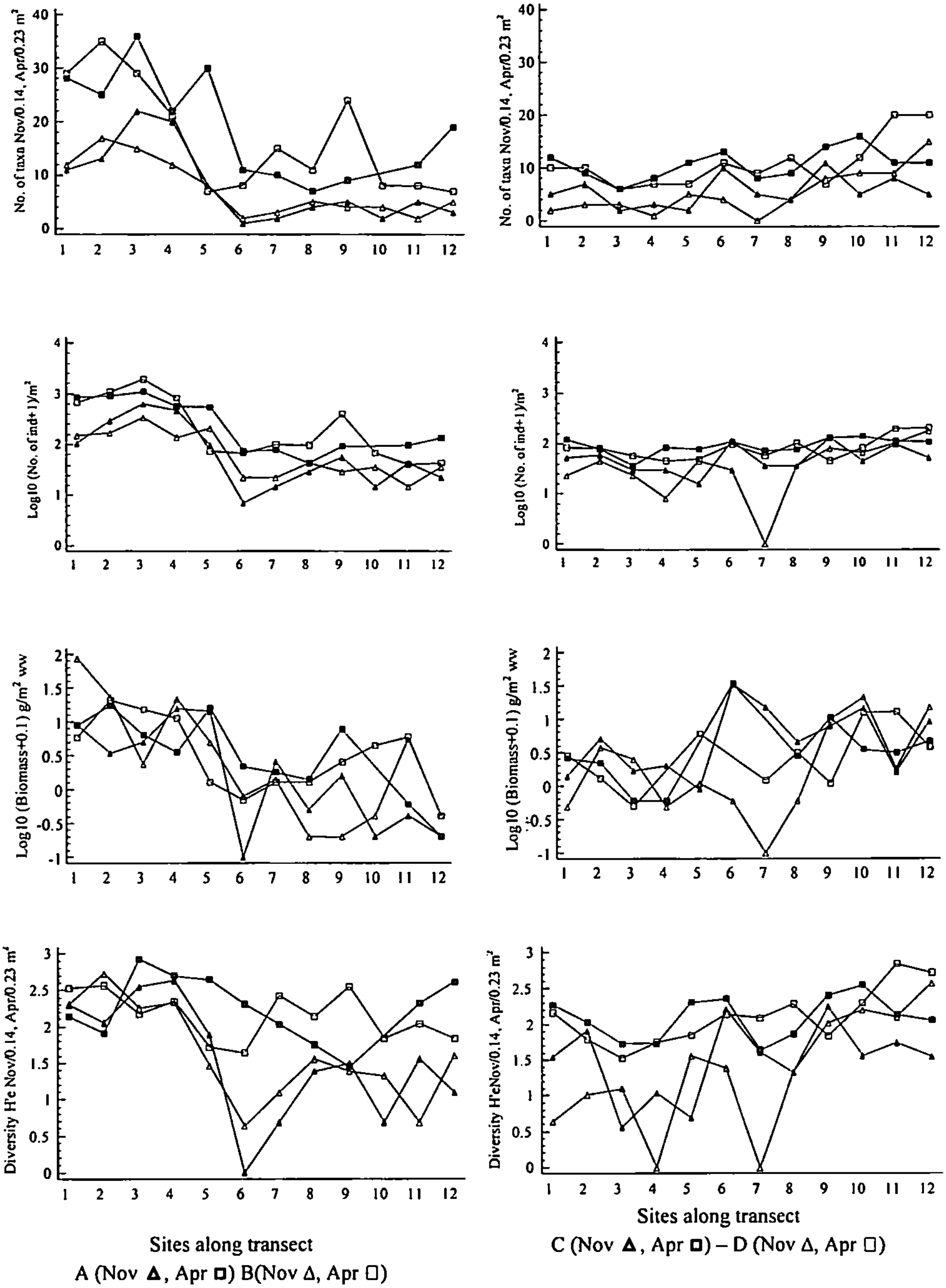


Figure 3.5. Large macrofauna patterns of biological measures at each station along transects A to D. Lines are as an aid to follow the transect. Biomass is wet weight (ww).

Table 3.1a. Best-fit models from stepwise multiple linear regression analysis to explain variation in the observations of number of taxa, log_{10} number of individuals, log_{10} Biomass; in terms of log_{10} depth, arcsin % of silt, arcsin % organic matter, mean grains size and sorting; at each fraction/season along transects A-B and C-D. * For non significant constants the residuals were normal and homocedastic, therefore the model was considered adequate

November-99 small macroinfauna transects A-B

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	13.0345	<0.0001	3.6802	<0.0001		
Organic matter	-59.8514	0.0073	-0.2828	0.0067	**None**	
Regression		0.0073		0.0067		
R-square	0.3087		0.3137			

November-99 small macroinfauna transects C-D

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	70.1262	0.0012	11.7943	0.0011		
% Silt	-1.1207	0.0026	-0.1726	0.0047	**None**	
Regression		0.0026		0.0047		
R-square	0.3439		0.3102			

November-99 large macroinfauna transects A-B

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	34.8177	<0.0001	7.2188	<0.0001	8.8920	0.0001
MGS	-3.3714	0.0095	-0.6057	0.0251	-1.5647	<0.0001
Organic matter	-1.1246	0.0445	-0.2523	0.0349		
Regression		<0.0001		<0.0001		<0.0001
R-square	0.7071		0.6779		0.5994	

November-99 large macroinfauna transects C-D

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	-24.2767	0.0101	-2.8721	0.1653*	-0.9967	0.8479*
Sorting	17.3603	0.0023	2.7347	0.0285	6.1728	0.0065
Depth					-2.8093	0.0367
Regression		0.0023		0.0285		0.0100
R-square	0.3513		0.2085		0.3690	

Table 3.1b. Best-fit models from stepwise multiple linear regression analysis to explain variation in the observations of number of taxa, log_{10} number of individuals, log_{10} Biomass; in terms of log_{10} depth, arcsin % of silt, arcsin % organic matter, mean grains size and sorting; at each fraction/season along transects A-B and C-D. * For non significant constants the residuals were normal and homocedastic, therefore the model was considered adequate

April 00 small macroinfauna transects A-B

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant			4.5007	<0.0001	-1.9958	0.0030
Organic matter	**None**		-0.3381	0.0139	-0.3693	0.0160
Regression				0.0139		0.0160
R-square			0.2663		0.2572	

April 00 small macroinfauna transects C-D

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant			-4.9013	0.1030*		
Depth	**None**		2.0373	0.0160	**None**	
Regression				0.0160		
R-square			0.2919			

April 00 large macroinfauna transects A-B

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	64.3817	<0.0001	108505	<0.0001	4.6562	0.0007
MGS	-7.1395	0.0001	-1.0723	<0.0001		
Depth					-1.3839	0.0003
Regression		0.0001		<0.0001		0.0003
R-square	0.5073		0.6894		0.4693	

April 00 large macroinfauna transects C-D

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	59.4896	0.0051	0.7959	0.3396*	4.0276	0.0228
Silt	-0.8667	0.0184				
MGS			1.227	0.0140		
Organic matter					-0.9246	0.0121
Regression		0.0184		0.0140		0.0121
R-square	0.2720		0.2913		0.3021	

Small macroinfauna. Along transects A-B during November 1999 (Table 3.1a), 30% of the total variation in number of taxa and log_{10} number of individuals respectively was explained by organic matter alone. During April 2000 (Table 3.1b) the same variable explained 25% of variation in number of individuals and biomass respectively (Figure 3.6). However, along transects C-D the explanatory variables varied with season. During November 1999 (Table 3.1a) percentage of silt explained above 30% of variation in number of taxa and number of individuals respectively. During April, (Table 3.1b) number of individuals presented a significant relationship with depth, otherwise no relationships were apparent (Figure 3.6).

Large macroinfauna. Along transects A-B during November 1999 (Table 3.1a), mean grain size and organic matter best explained the variation in number of taxa and individuals (70% of variability respectively). However, only mean grain size best explained the variation in biomass (59%). During April 2000 (Table 3.1b), mean grain size alone explained 50% and 68% of variation in number of taxa and individuals respectively. Depth explained 46% of variation in biomass (Figure 3.7). Along transect C-D the explanatory variables changed with season. During November 1999 (Table 3.1a), sorting of sediment was the only variable included in the model that explained only 35% and 20% of variation in number of taxa and individuals respectively. Sorting and depth best explained variation in biomass data. During April 2000 (Table 3.1b) percentage of silt explained 27% of the total variation in number of taxa, mean grain size explained 29% of variation in number of individuals, and percentage of organic matter best explained 30% of variation in biomass (Figure 3.8).

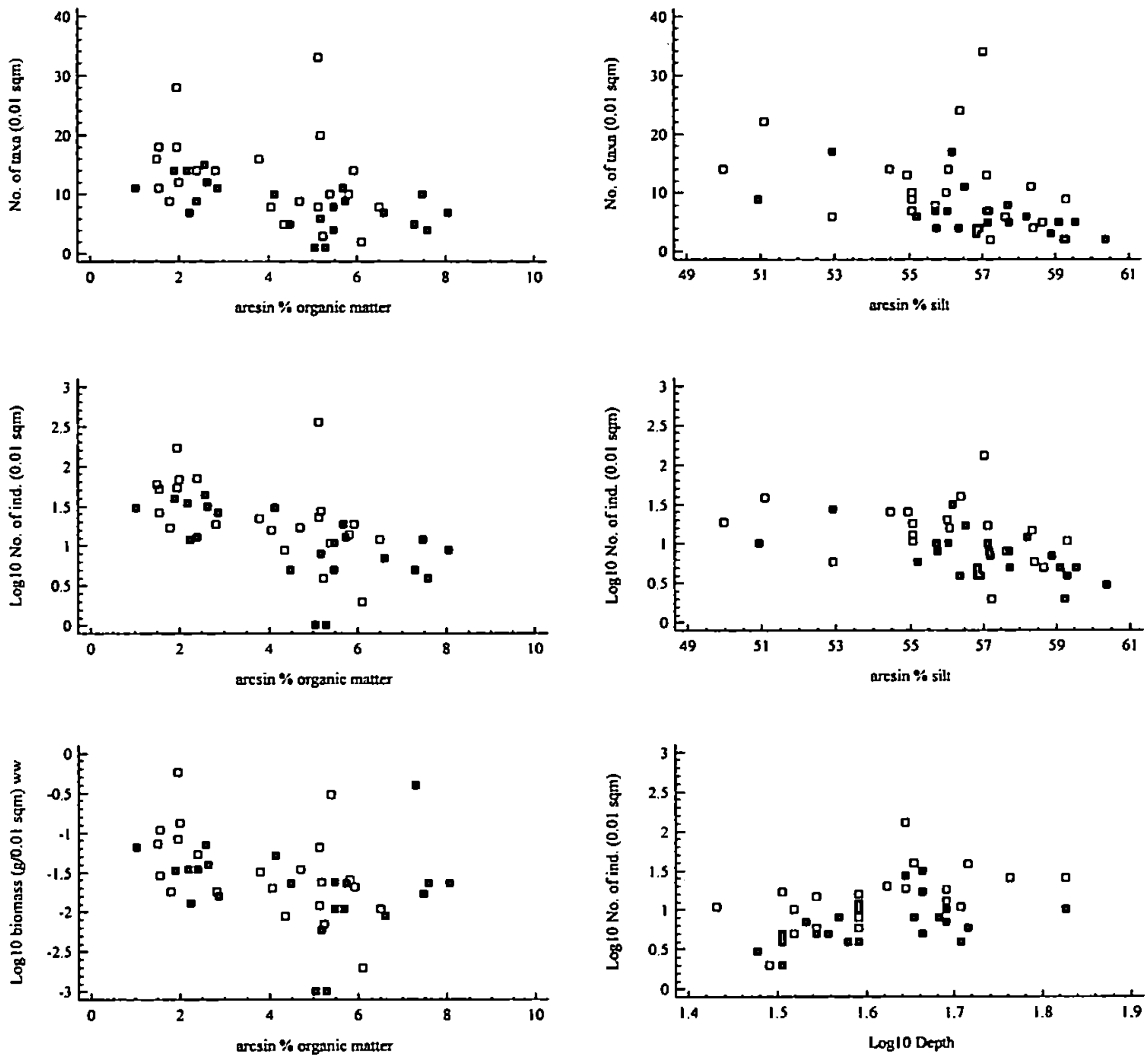


Figure 3.6. Scatterplots of small macroinfauna biological measures against best explanatory variables selected by the multiple regression analysis (left column data along transect A-B, right column data along transect C-D; during November 1999 ▪ and April 2000 □)

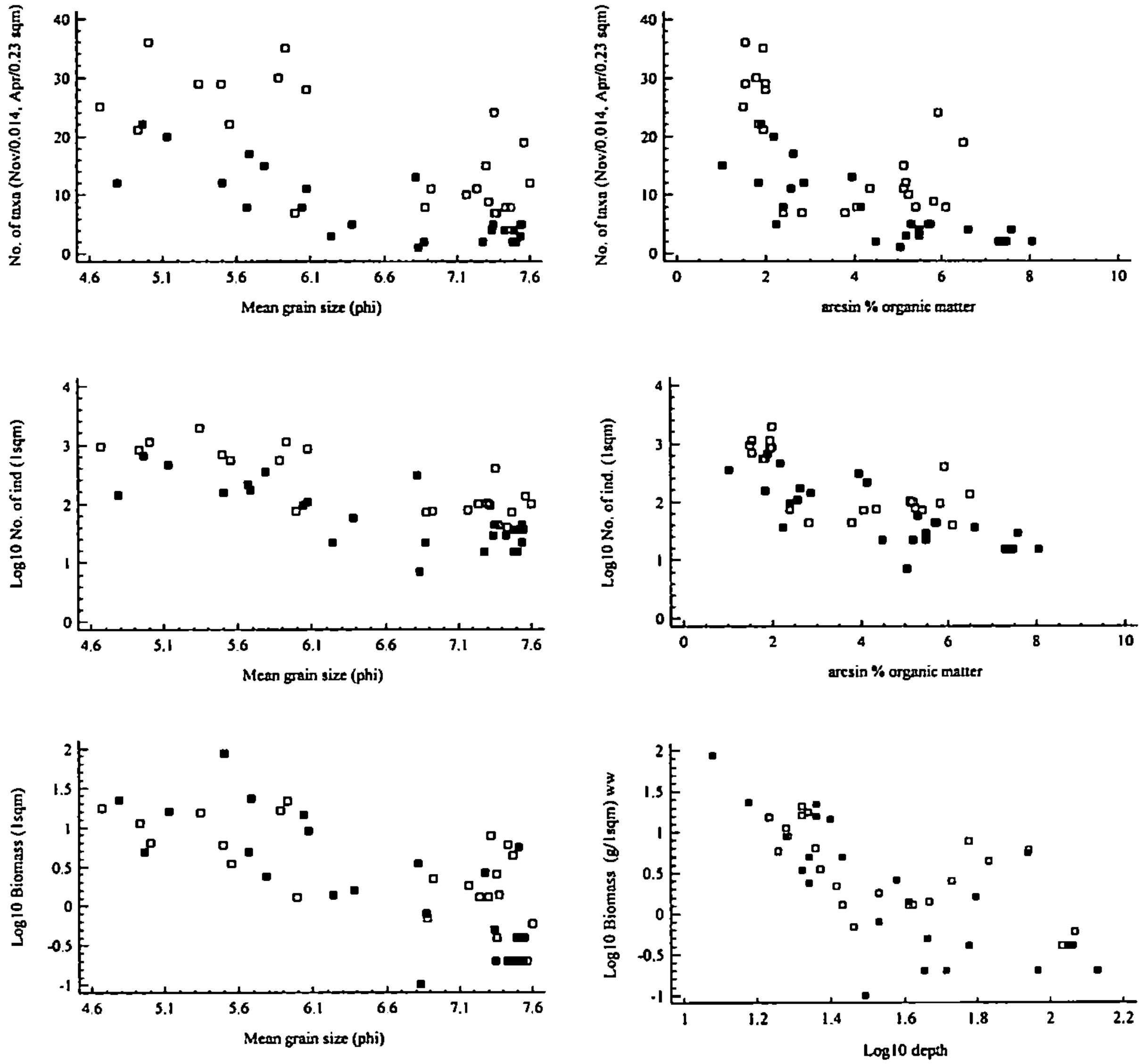


Figure 3.7. Scatterplots of large macroinfauna biological measures against best explanatory variable from the multiple linear regression analysis along transects A-B (November 1999 ■ and April 2000 □).

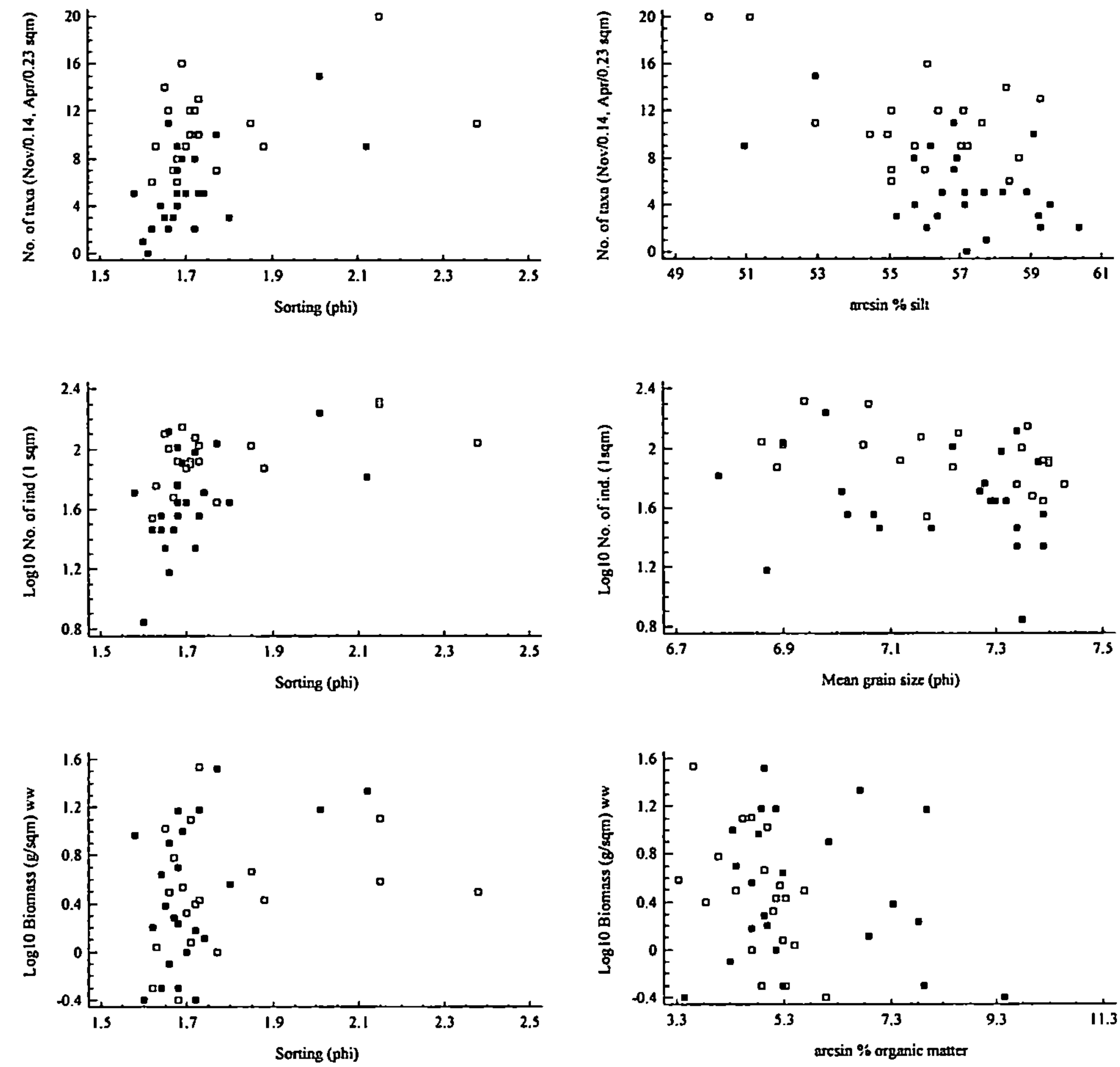
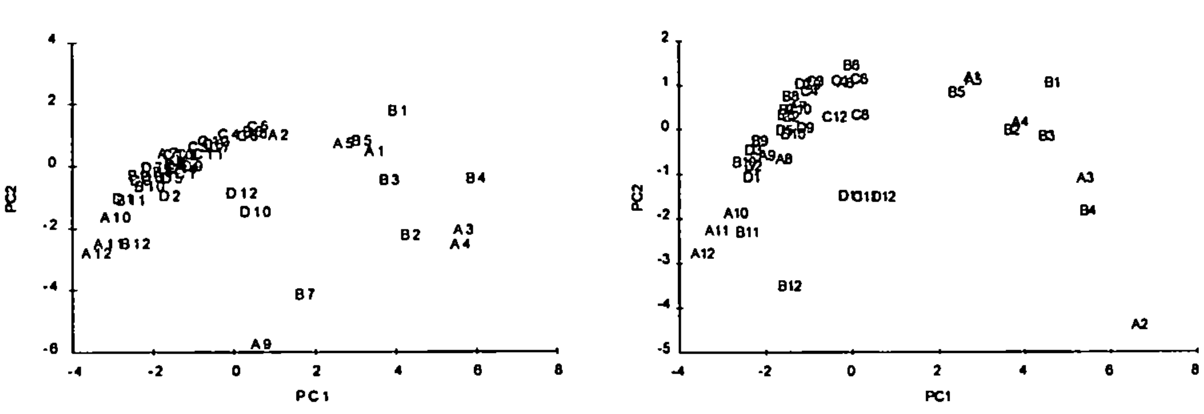


Figure 3.8. Scatterplots of large macroinfauna biological measures against best explanatory variable from the multiple linear regression analysis along transects C-D (November 1999 ▪ and April 2000 ▫)

Multivariate analyses

<u>Principal components Analysis</u>

The environmental features of the sampled sites during each season are summarised by the PCA of the 10 measured natural variables (Figure 3.9). During November PC1, explains 60% of the variation and relates to increasing values from left to right of sand, mean grain size, carbonate content and a weaker contribution of sorting of sediment. Salinity, clay content, surface area of sediment and organic matter also have an important contribution, but with the opposite trend, followed by content of silt with a smaller influence. The second PC axis explains 21% of variation dominated by silt, sorting and a weaker contribution of depth that decreases in magnitude from bottom to top of the figure (Table 3.2a). During April, PC1 explains 67% of variation with a similar pattern of increasing values from left to right of sand, mean grain size, carbonate content and a weaker contribution of sorting of sediment. In November, salinity demonstrated the opposite trend to April, reflecting the decrease in river discharge after the rainy season (Table 3.2b). The second PC axis explains 18% of variation during April related to the same variables as in November (Table 3.2b). NB note that shallow and deep stations along transect A-B separate out from all the rest indicating a clear natural gradient.



November 1999 April 2000

Figure 3.9. PCA ordination plot of the 2 first PCs of 10 transformed natural environmental variables by season based on normalised Euclidean distances. Numbers 1-12 represent stations along transects A-D.

Table 3.2a. Eigenvalues, percentage of variation explained and coefficients in the linear combination of ten variables making up the first two PC for 48 stations sampled during November 1999.

	PC1	**PC2**
Eigenvalues	6.08	2.16
% of variation	60.8	21.6
Variables/coefficients		
Depth m	-0.275	**-0.345**
Log (salinity ups)	**-0.315**	-0.269
Arcsin (% sand/100)	**0.344**	**-0.339**
Arcsin (% silt/100)	-0.194	**0.579**
Arcsin (% clay/100)	**-0.385**	-0.148
Log (surface area m^2 gm^{-1})	**-0.375**	-0.059
Mean grain size (phi)	**-0.395**	0.080
Sorting (phi)	0.172	-0.50
Arcsin (% organic matter/100)	**-0.300**	-0.009
Arcsin (% carbonate/100)	**0.324**	0.266

Table 3.2b. Eigenvalues, percentage of variation explained and coefficients in the linear combination of ten variables making up the first two PC for 48 stations sampled during April 2000.

	PC1	**PC2**
Eigenvalues	6.70	1.85
% of variation	67	18.5
Variables/coefficients		
Depth m	-0.260	**-0.440**
Log (salinity ups)	0.226	0.269
Arcsin (% sand/100)	**0.360**	-0.249
Arcsin (% silt/100)	-0.217	**0.583**
Arcsin (% clay/100)	**-0.363**	-0.207
Log (surface area m^2 gm^{-1})	**-0.367**	-0.118
Mean grain size (phi)	**-0.380**	0.050
Sorting (phi)	0.255	**-0.470**
Arcsin (% organic matter/100)	**-0.354**	0.031
Arcsin (% carbonate/100)	**0.322**	0.226

Multi-Dimensional Scaling

The stress values for all the 2-d MDS plots of transformed abundance and biomass are above 0.2 indicating difficulty in representing the multivariate patterns in 2 dimensions. To help to visualise the overall pattern for the large macrofauna in November, samples A6, D4 and D7 were removed due to extremely low numbers and biomass that over-influenced the 2-d display (A6 and D4 had one family and one individual each and D7 had no fauna at all). Unlike the clear patterns for environmental variables (PCA), none of the ordination plots of abundance or biomass for any fraction and season presented either a clear pattern of linear variation along the transects or a consistent pattern of clustering. The only exceptions were the shallow stations A1-A5 and B1-B5. These were the most similar in community composition and tended to cluster in the centre of the plots.

The plots of small macroinfauna from November (Figure 3.10) represent a pattern of increasing dissimilarity radiating from the centre. Sites located at the outer edge are the most impoverished, with densities ranging from 1 to 4 individuals/0.01 m^2, low biomass and only 1-2 different families. The same pattern is observed in April (Figure 3.11), but densities, biomass and number of taxa of the stations scattered on the external edge of the plot were higher, ranging from 2-9 ind/0.01m^2 and 2-10 families per site.

For the large macrofauna from November (Figure 3.12), the most impoverished sites (beside the three already mentioned) were scattered around the top edge of the plot with densities of 2-4 ind/0.14 m^2 or 14-28 ind/m^2 and 2 families per site. A similar pattern was evident from April (Figure 3.13), with impoverished sites spread around the external edge. These sites are highly dissimilar to others since they have few taxa in common. Sites from the inner shelf are all clustered together.

The one-way ANOSIM test for differences between seasons for transformed abundance of small macroinfauna and for standardised abundance for large macroinfauna, showed slight, yet significant differences in community composition between the rainy and northers seasons (small macroinfauna: $R = 0.085$, $p=0.001$; Large macrofauna: $R = 0.091$, $p=0.001$ respectively).

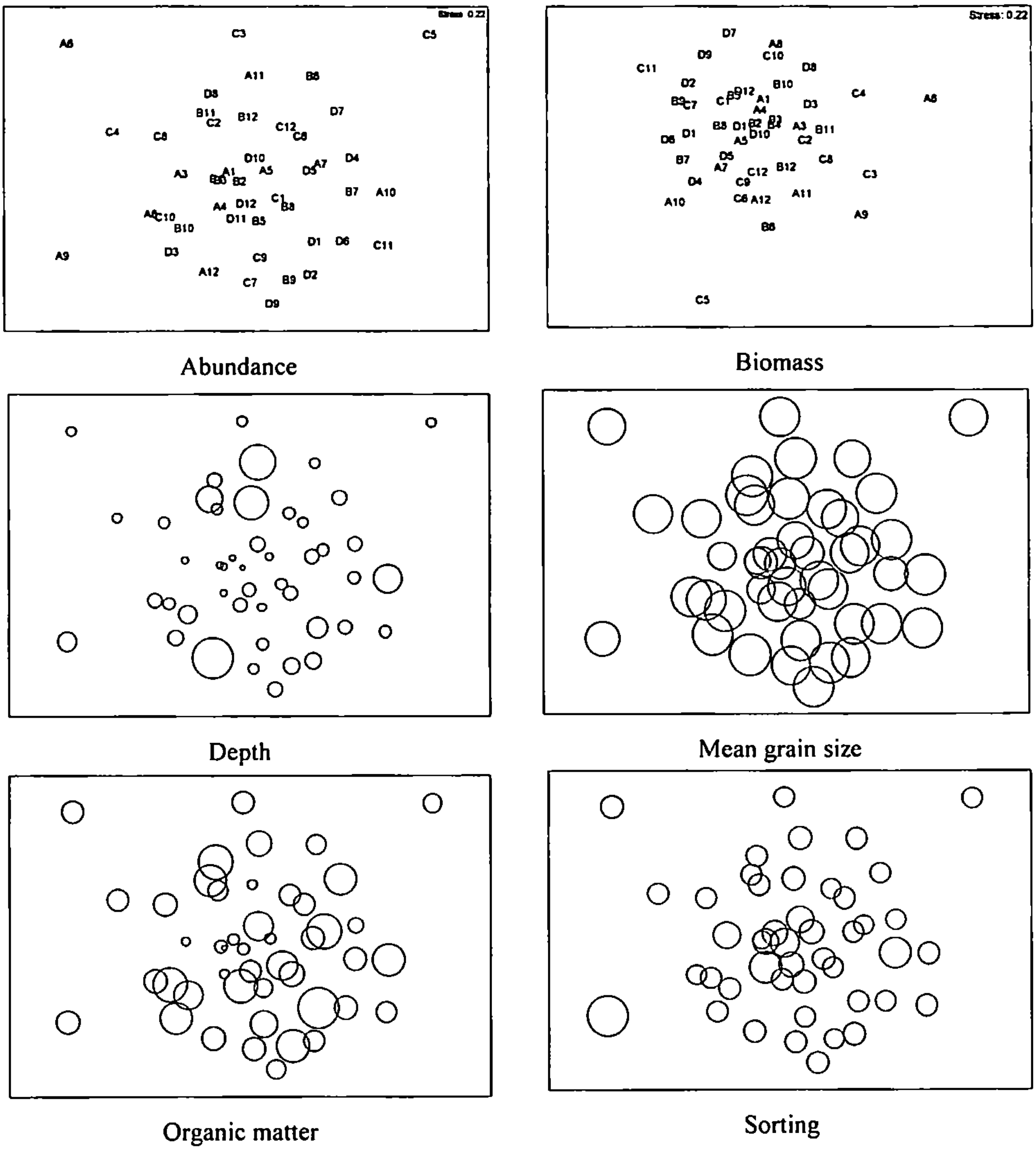


Figure 3.10. 2-d MDS ordination plots of small macroinfauna during November 1999 based on Bray-Curtis similarities of abundance and biomass fourth root transformed with superimposition of selected natural variables on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

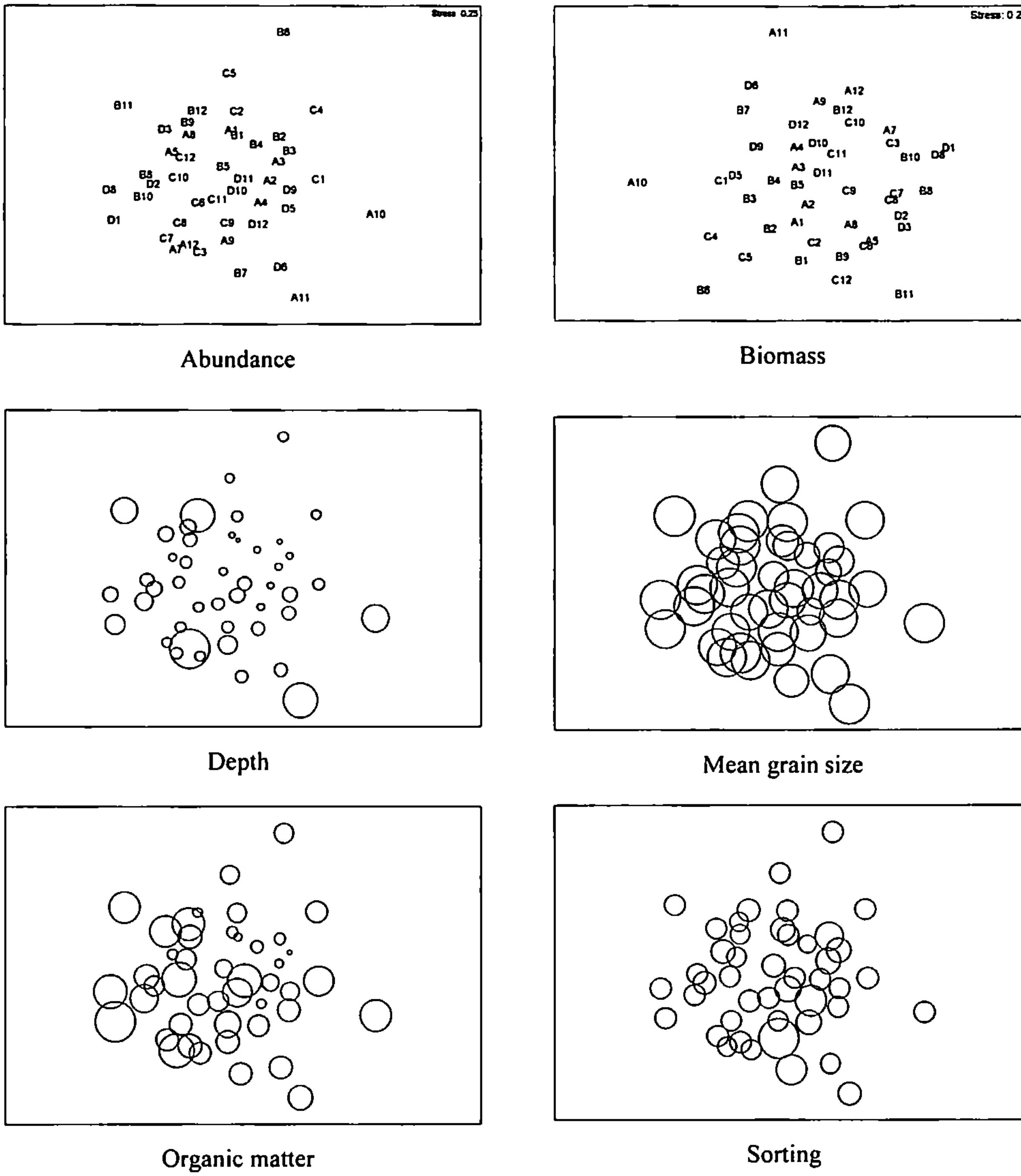


Figure 3.11. 2-d MDS ordination plots of large macroinfauna during November 1999 based on Bray-Curtis similarities of abundance and biomass fourth root transformed with superimposition of selected natural variables on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

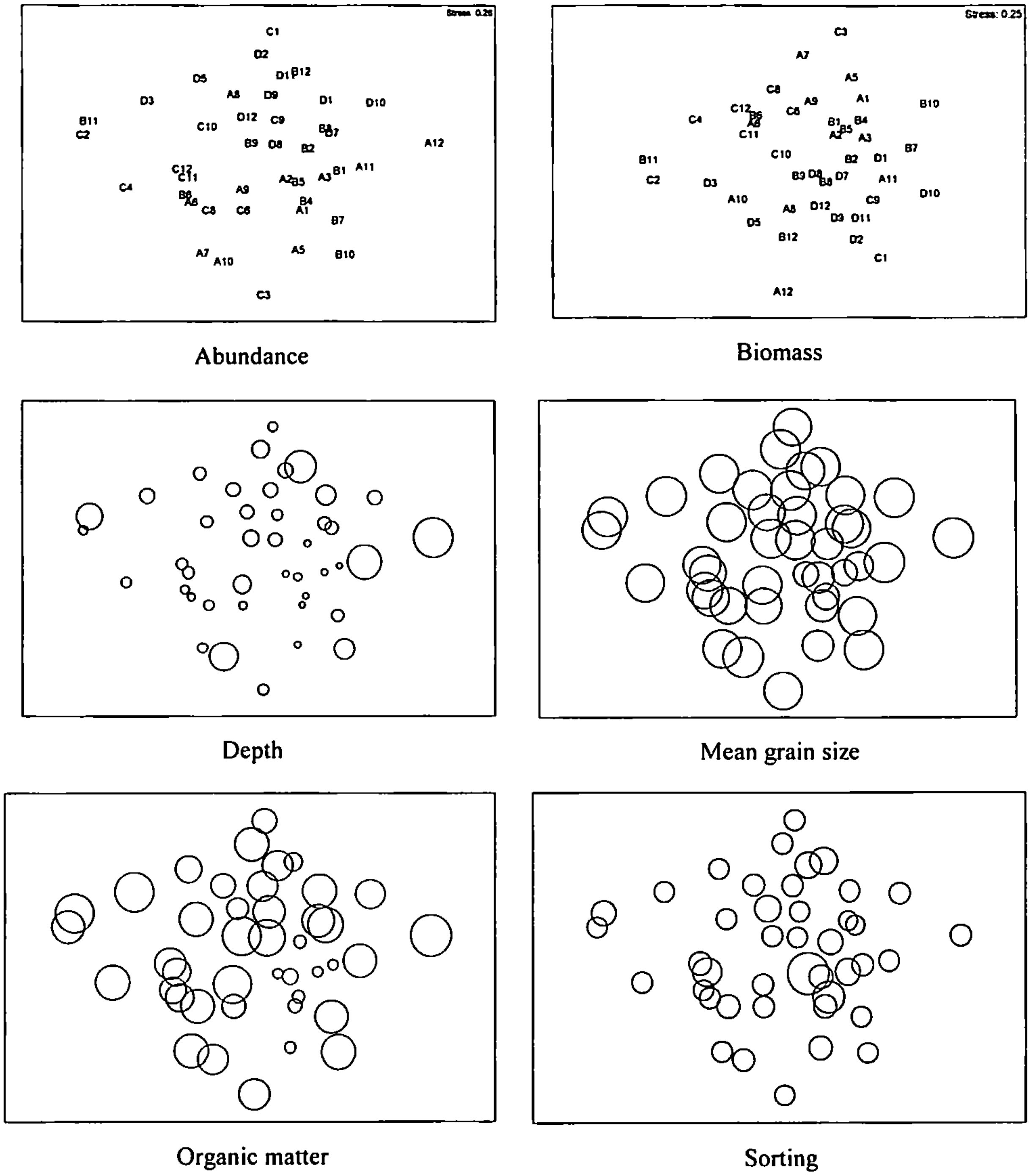


Figure 3.12. 2-d MDS ordination plots of small macroinfauna during April 2000 based on Bray-Curtis similarities of abundance and biomass fourth root transformed with superimposition of selected natural variables on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

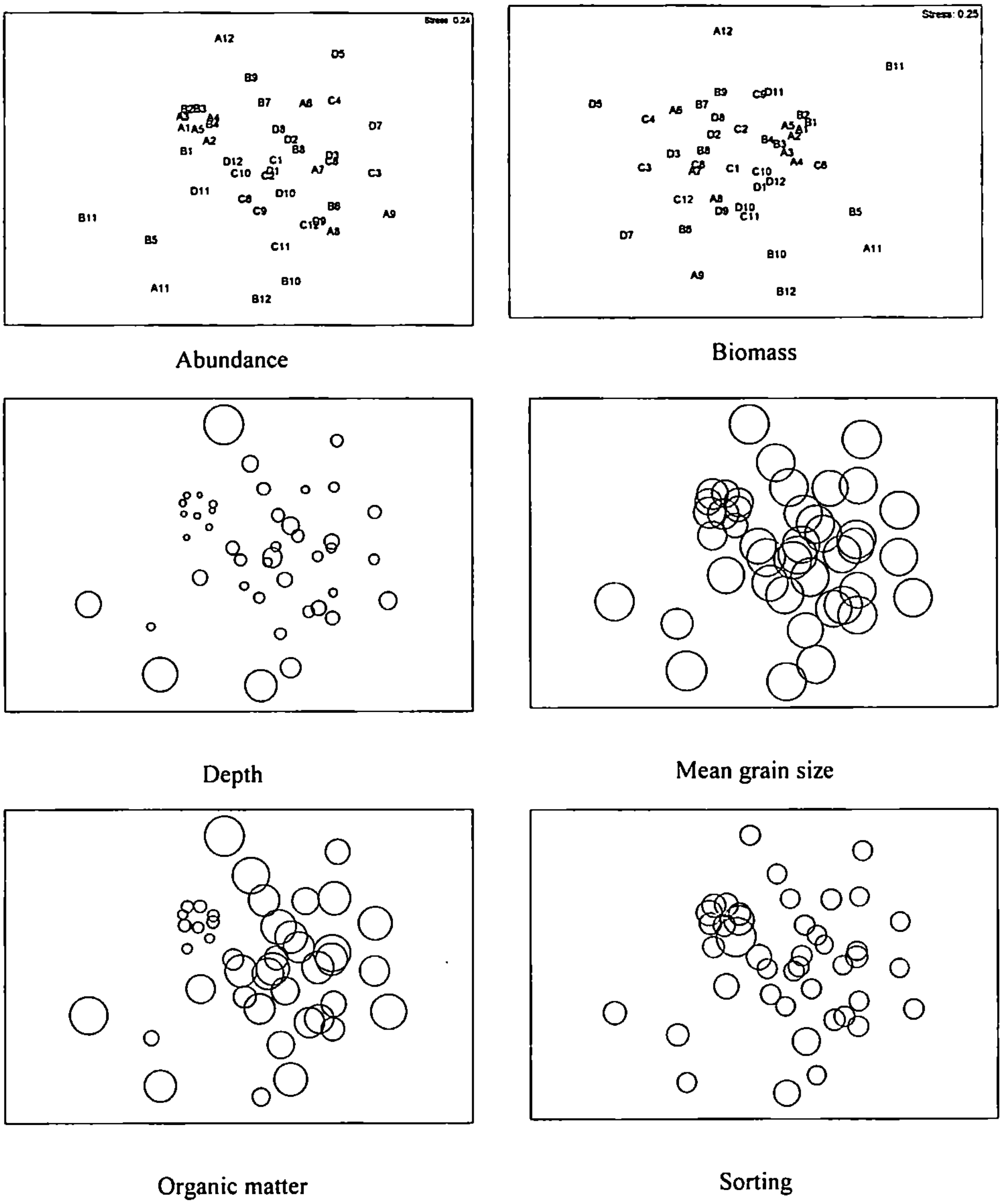


Figure 3.13. 2-d MDS ordination plots of large macroinfauna during April 2000 based on Bray-Curtis similarities of abundance and biomass fourth root transformed with superimposition of selected natural variables on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

Linking the multivariate patterns of biota to environmental variables

The superimposition of the natural variables on the ordination plots for transformed abundance showed no relationship with either small or large macroinfauna during any season (Figure 3.10-3.13) with the single exception of large macroinfauna and organic matter during April 2000.

BIOENV analysis: Spearman rank correlations between the similarity matrices of fauna and PCA ordinations of a set of 5 variables (same as those for the regression analysis) are given in Table 3.3. Depth was the single best explanatory variable for the biotic pattern of small and large macrofauna during both seasons. However, for the large macrofauna the highest correlation was with a combination of depth and organic matter for both seasons (Table 3.3).

Table 3.3. Relationship between environmental variables and fauna using BIOENV analysis, the best combination of one to three variables that best explain the faunal patterns are given for each fraction/season. The correlation coefficient (r_s) is for Spearman rank correlation.

Nov. small macroinfauna		Nov. large macroinfauna		April small macroinfauna		April large macroinfauna	
Variables	r_s	Variables	r_s	Variables	r_s	Variables	r_s
Depth, Silt, Sorting	0.032	Depth, Silt, Organic matter	0.206	Depth, Mean grain size, Organic matter	0.100	Depth, Mean grain size, Organic matter	0.399
Depth, Silt	0.053	Depth, Organic matter	**0.242**	Depth, Organic matter	0.158	Depth, organic matter	**0.472**
Depth	**0.085**	Depth	0.237	Depth	**0.253**	Depth	0.445

SIMPER analysis

Table 3.4a-b contain the most important families that contribute up to 60% of the overall dissimilarity between seasons for each fraction. For both small and large macroinfauna, most of these families had low abundance during November (rainy season) and increased during April ('northers' season). There were no good discriminatory families for either fraction, as indicated by the low dissimilarity/standard deviation ratio. All families have an uneven distribution, being numerous in some samples but rare or absent in others within a particular season. The first five most important families for the small macroinfauna were mainly polychaetes (four out of five), but for the large macroinfauna a wider range of taxonomic groups were represented (e.g. crustaceans, polychaetes, nemertean and ophiuroid). Figures 3.14 and 3.15 display the pattern of densities of two of the first five most important families that contribute to the total overall dissimilarities. These were chosen as they have high average abundance per station. For the small macroinfauna, they were Spionidae and Capitellidae and for the large macroinfauna, Goneplacidae and Spionidae. Although on average the densities were higher during the 'northers' season, the pattern along the transects is inconsistent, which is reflected in the low ratios of average dissimilarity/standard deviation in Table 3.4.

Table 3.4a. Small macroinfauna breakdown of average dissimilarity between seasons into contributions up to 60% from the most important families. Total average dissimilarity = 82.54

	Rainy	Northers			
Families	Av.Abund	Av.Abund	Av.D	AvD/SD	AvD Cum.%
Spionidae	1.22	2.64	3.83	0.98	4.64
Linneidae	0.74	1.26	3.3	0.92	8.63
Lumbrineridae	1.07	1.19	3.26	0.93	12.59
Nephtyidae	0.33	1	3.22	0.8	16.49
Capitellidae	1.26	3.57	3.21	1.01	20.38
Apseudidae	0.67	3.71	2.87	0.8	23.85
Corbulidae	0.46	2.21	2.41	0.73	26.77
Nanastacidae	0.35	0.95	2.27	0.71	29.51
Alpheidae	0.46	0.29	2.19	0.73	32.16
Myscidacea	0.2	0.67	2.17	0.65	34.79
Goneplacidae	0.2	0.4	2.09	0.65	37.33
Tellinidae	0.22	1.43	2.08	0.7	39.84
Paraonidae	0.39	1.29	1.92	0.63	42.16
Liljeborgidae	0.15	0.52	1.81	0.64	44.36
Ampeliscidae	0.24	0.36	1.8	0.73	46.54
Onuphidae	0.24	0.38	1.8	0.68	48.72
Oedicerotidae	0.17	0.45	1.73	0.62	50.82
Cirratulidae	0.24	0.48	1.7	0.7	52.87
Corophidae	0	0.48	1.67	0.61	54.9
Aspidosiphonidae	0.24	0.33	1.66	0.6	56.91
Cossuridae	0.43	0.4	1.65	0.6	58.91
Lyssianasidae	0.22	0.33	1.61	0.5	60.86

Table 3.4b. Large macroinfauna breakdown of average dissimilarity between seasons into contributions up to 60% from the most important families. Total average dissimilarity = 72.60

	Rainy	Northers			
Families	Av.Abund	Av.Abund	Av.D	AvD/SD	AvD Cum.%
Goneplacidae	1.19	4.21	3.67	1.01	5.06
Alpheidae	0.89	2.74	3.57	1.11	9.98
Spionidae	1.15	8.63	3.46	1.05	14.74
Linneidae	0.96	2.65	3.42	1.09	19.45
Amphiuridae	0.51	1.3	3.32	1.1	24.03
Onuphidae	0.38	1.63	3.19	1.06	28.43
Capitellidae	1.21	6.26	3.14	1.05	32.75
Lumbrineridae	0.36	1.84	2.93	1.09	36.78
Nephtyidae	0.26	0.95	2.76	0.95	40.59
Aspidosiphonidae	0.36	2.21	2.56	0.92	44.11
Maldanidae	0.43	1.19	2.38	0.81	47.39
Apseudidae	0.55	11	2.18	0.79	50.39
Pinnotheridae	0.34	0.98	2.13	0.76	53.33
Callianasidae	0.3	0.86	1.9	0.71	55.95
Paraonidae	0.3	1.93	1.7	0.77	58.3
Tellinidae	0.17	0.77	1.66	0.67	60.59

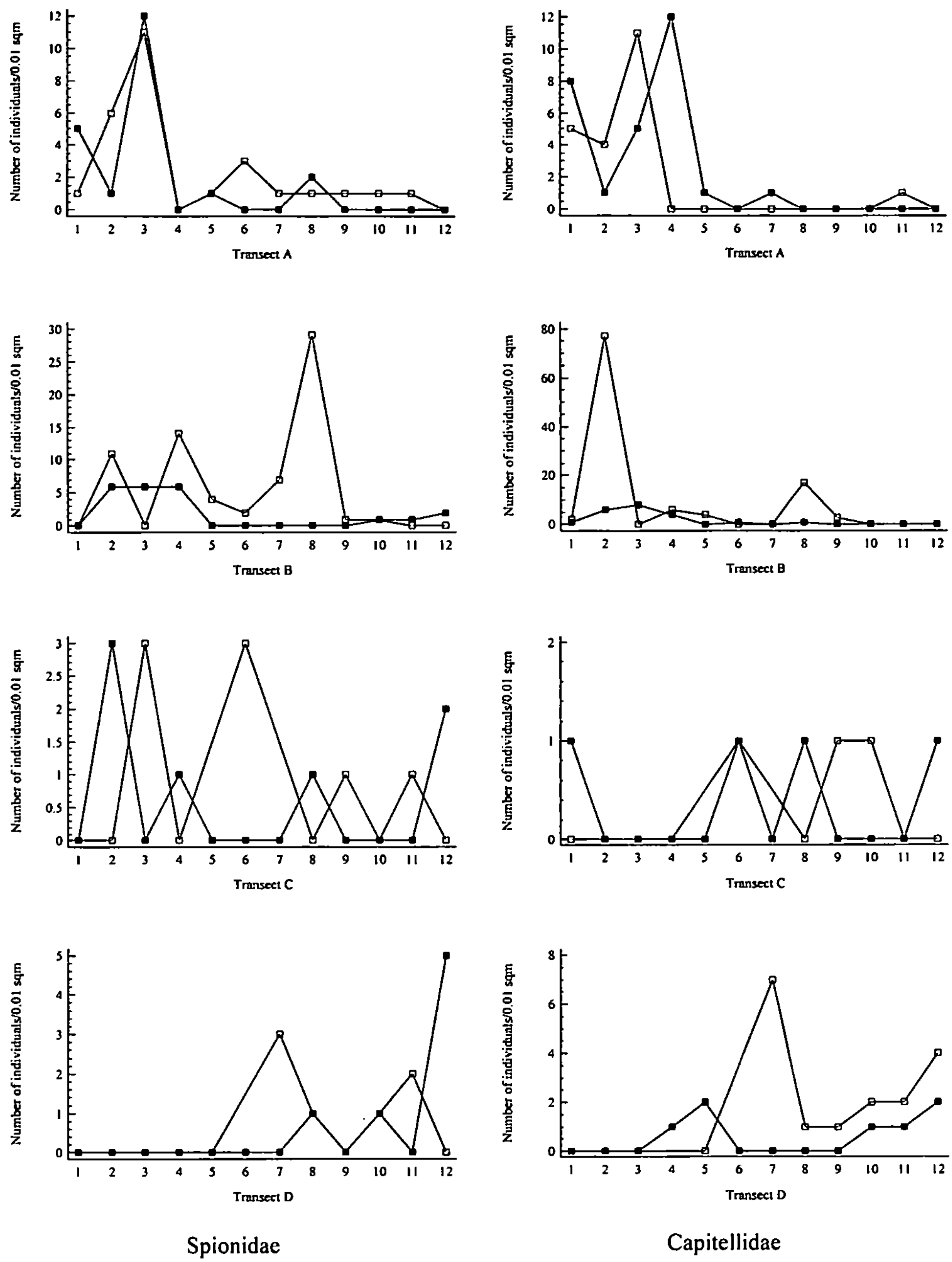


Figure 3.14. Pattern along transects of number of individuals/0.01 m^2 (times 100 for 1 m^2) of spionids and capitellids worms from the small macroinfauna fraction (■-November 1999, □-April 2000)

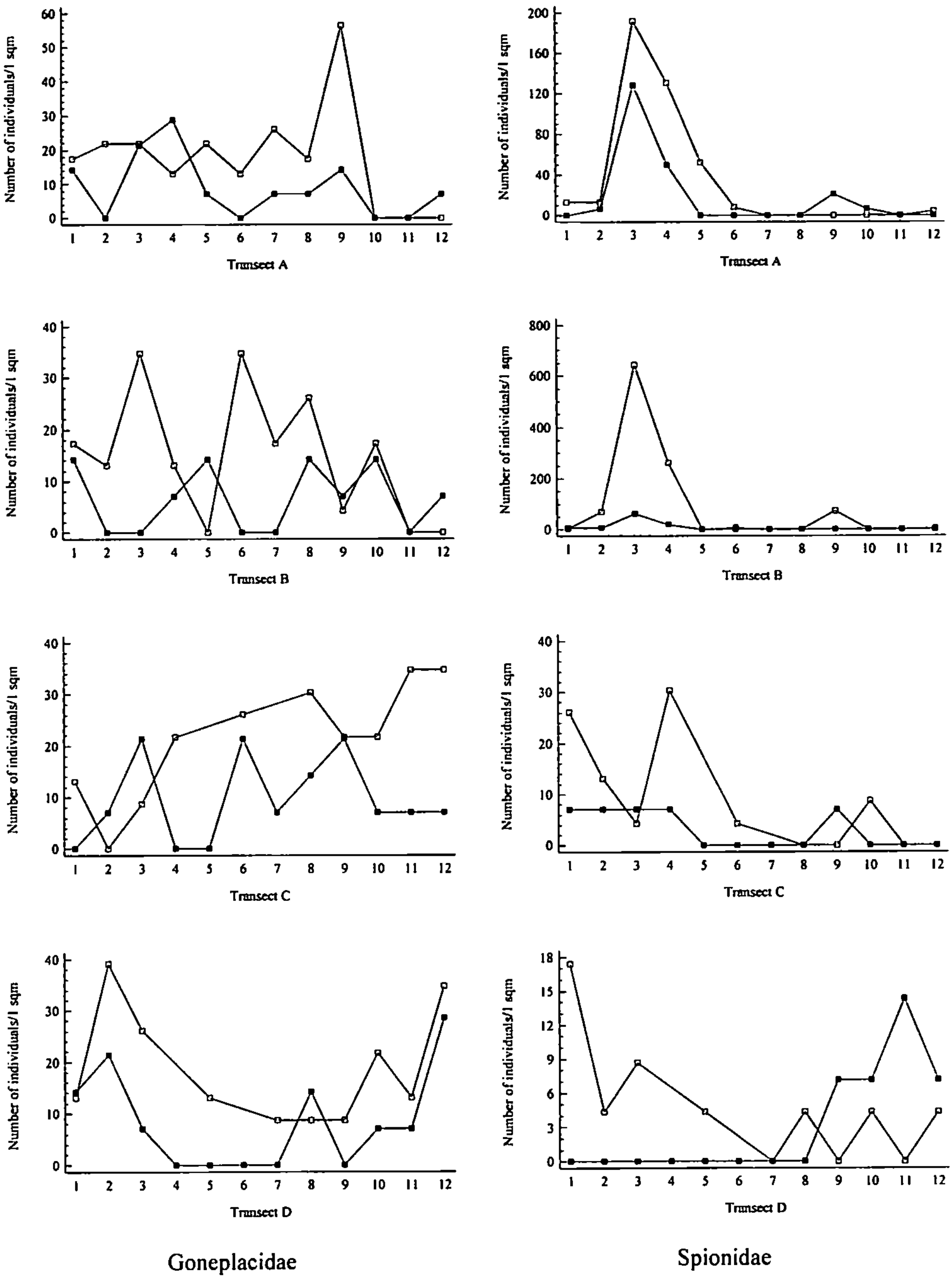


Figure 3.15. Pattern along transects of number of individuals/1 m^2 of goneplacid crabs and spionid worms from the large macroinfauna fraction (▪-November 1999, □-April 2000)

Discussion

Spatial patterns of natural environmental variables reflected the across-shelf changes in slope. Depositional/erosional events can be followed along transects (markedly along A-B) by changes in mean grain size, carbonate content and variability in bulk organic matter. This reflects winnowing of medium to fine silts and clays from the inner-shelf (stations <30m deep) and sequential deposition offshore, as well as changes in the along-shelf main current flow during autumn and winter (Rosales-Hoz *et al.* 1999). The comparatively small temporal variation in sediment variables (when compared with large-scale patterns in Chapter 2) indicates the general homogenous nature of the seabed of the transitional shelf in the Southern GoM. However, temporal variation in water column instability is marked and reflected in salinity changes on the inner shelf. Water column instability in the area occurs periodically, driven by the interaction of rainy and "northers" season (Soto & Escobar-Briones 1995, Fuentes-Yaco *et al.* 2001). Temporal and spatial patterns of small and large macroinfauna covaried with shelf-wide physical processes, following the distribution of sediment type, depositional regime and intensity of natural disturbance. However, spatial patterns were evidently more variable away from the inner shelf and therefore do not reflect the homogenous muddy sedimentary environment that exists along transects C-D, for example. Low values of biological measures recorded at most of the sites after the heavy rainy season indicate that temporal variability is associated with periodically repetitive processes of water column instability, sediment load and, perhaps, fluid mud generation (Rezak *et al.* 1990).

Continental shelves influenced by large rivers exhibit clear spatial and temporal gradients of biological measures moving away from the deltaic region and from low to high flow periods. Models of community structure in relation to gradients of deposition off large rivers have proposed in general three areas across the shelf. Firstly, the delta and inner shelf area have an impoverished community due to depositional and erosional events and high content of refractory organic matter. Secondly, a middle shelf area where lower rates of deposition and higher food quality from pelagic source result in a high-density community. Finally, there is the oligotrophic outer shelf, which has reduced benthic standing stocks although diversity is high (Rhoads *et al.* 1985). Reported densities of small macroinfauna in such regions range from 200-7600 ind m^{-2} on the Amazon Shelf (Aller & Stupakoff 1996), 86-5555 ind m^{-2} on the Fly River shelf (Alongi *et al.* 1992) and up to <3000-20000 ind m^{-2} on the Changjiang delta and adjacent shelf (Rhoads *et al.* 1985). Deltaic areas and mobile muddy sediments can suffer total elimination of infauna and generally are depauperated zones during high flow (Saoyuan & Yongting 1985, Aller & Aller 1986). Densities of small macroinfauna in muddy sedimentary environments from the NW GoM, and thus out of the direct influence of rivers, tend to decrease with depth (Flint 1981, Flint & Rabalais 1981) and are within the range of 370-67700 ind/m^2 (Alexander *et al.* 1981). These depth gradients exhibit a sharp decline after the inner shelf (approximately 20 to 30 metres depth) coincident with marked changes in shelf topography, the area influenced by river runoff, an interaction of reverted flow on the general circulation pattern and the major influence of winter stress (Rabalais 1990).

Small macrofauna densities recorded in this study (100-35800 ind/m^2) are within the range from other shelves influenced by river runoff, but relatively low compared with the Northern GoM. The study area did not include the deltaic region, but all the same there is no clear spatial gradient in faunal variables moving away from the river's influence (e.g. the distribution of biological variables along transects CD) and the most impoverished sites do not correspond to those closest to the river influence. Inner-shelf peaks in biomass and densities of macroinfauna, and the negative association with depth, resembles previous studies in both the Southern and Northern GoM and have been explained in terms of food supply from the overlying water column. However, biomass did not exhibit any clear temporal pattern from the rainy to the 'northers' seasons, contrary to that reported by (Soto & Escobar-Briones 1995). The absence of depth-related zonation from 30-135 metres and the increases in variability both in densities and community composition in the Southern GoM are in contrast to the even distribution and high diversities that result from greater stability in hydrological variables in the Northern Gulf (Alexander *et al.* 1981). The observed pattern of increased variability in this study might be related to a sequence of disturbance from river runoff and winter storms, but the presence of oil related activities as a putative influence on the benthic community can not be disregarded and will be investigated further in Chapter 4.

Results from the regression analysis indicate a negative relationship between the biological variables and content of bulk organic matter and mean grain size along transects A-B. An increased input of fine sediments from terrestrial origin is concomitant with an increase of highly refractory organic matter and in the southern GoM this can amount for up to 50% in continental shelf sediments (Hedges & Parker 1976). It is then considered that the negative relationship is a result of disturbance caused primarily by river runoff. Temporally, community structure is greatly affected during the peak of the river discharge, with a subsequent increase in densities of numerous opportunistic species (Aller & Stupakoff 1996). This temporal pattern has been linked on one hand to the presence-absence of disturbance (Aller & Aller 1986) and on the other to the lagged used of the organic input by the benthic community (Salen-Picard *et al.* 2002). The area of study did not include the deltaic area, but the middle and outer shelf are well represented. However, the middle shelf does not seem to fit the above general model since very low values of all biological measures in general were recorded. Nonetheless, regression analyses indicated that the amount of silt and sorting of sediment can explain part of the variation. This is coherent with the supposition of disturbance from river runoff, as increasing silt and decreasing sorting of sediments could relate to erosional and depositional events along the shelf.

The ANOSIM results indicated significant but very small seasonal differences in community composition for both small and large macroinfauna. These differences were produced by changes in the abundance of several families of polychaete (Capitellidae, Spionidae, Cirratulidae, Paraonidae, Lumbrineridae) that are know to contain opportunistic species, their populations dramatically increasing across the inner shelf four months after the rainy season had ended. Some other stations (B8 and D7) do present the characteristic peak of opportunists with numerous copepods, ostracods, juvenile bivalves, spionid and paraonid poychaetes within the small macrofauna. However, this pattern was not evident along transects C-D, where no gradient of biological variables was detected.

Natural disturbance related to river runoff can be extensive, but has a gradational influence that decreases moving away from the source. From previous studies it is known that clay and carbonate content represent different sources of sedimentary material, as reflected by the along-shelf east to north east gradient on the inner shelf (<30m depth) (Gutierrez-Estrada & Galaviz-Solis 1991, Rosales-Hoz *et al.* 1999). It has been suggested that benthic community structure and function varies along the same gradient, with increasing densities and biomass towards the carbonate shelf (Yañez-Arancibia & Sanchez-Gil 1983, Soto & Escobar-Briones 1995, Soto *et al.* 1998), so it can be speculated that stations on the inner shelf are part of this along-shore spatial gradient, which showed marked temporal changes. Under this assumption a similar gradient would also be expected along the middle shelf, but this gradient appears to be broken along transects C-D. This is reflected by the multivariate patterns of the MDS plots for both abundance and biomass where variability along transects C-D dominates the overall pattern. The results of the BIOENV analysis also demonstrated the lack of defined spatial gradients, particularly for the small macrofauna during November. Although depth was the single variable that represents the best fit, the best correlation value was only 0.4 (for the large macroinfauna in April) and little improvement was achieved by adding variables to explain the multivariate pattern.

Thus natural disturbance produces an overall impoverishment of the area immediately after the peak of the rainy season, with a clear response of opportunistic species as a result of absence of disturbance and the increasing supply of organic material. However, the general spatial patterns of macrobenthic community structure across and along the shelf in relation to changes in depth and distance to river influence as described in other areas, (Alexander *et al.* 1981, Rhoads *et al.* 1985, Aller & Aller 1986, Alongi *et al.* 1992, Coleman *et al.* 1997, Salen-Picard *et al.* 2002) were not observed in the Southern GoM. SIMPER analysis showed that all the most important families contributing to the overall dissimilarities between seasons increased in abundance from the rainy to the 'northers' season. These families (such as capitellids, spionids, paraonids) include opportunistic species and had their highest abundances on the inner shelf. However, the spatial patterns of spionid and capitellid worms and goneplacid crabs also suggested a breakdown of the general model of densities of macroinfauna across the shelf and along areas of river influence. This assumption is based on increased variability, and absence of several families, observed particularly at the crossing of the transects, where intense oil activities have been developed for more than 20 years. The present sampling design attempted to control for the main sources of natural disturbance in the area by sampling after the rainy and winter storms season, as macroinfauna is known to present an integrated response over time. The temporal changes indicate disturbance effects from river runoff, but the spatial changes were more complicated than could be explained purely in terms of natural disturbance. These changes do not follow either the natural change in topography across the shelf or the putative patterns expected when moving away from river influence. It is therefore necessary to explore defined spatial changes in relation to a putative source of anthropogenic disturbance.

CHAPTER 4

ASSESSING THE IMPACT OF OIL RELATED ACTIVITIES ON THE BENTHIC MACROINFAUNA OF THE CAMPECHE BANK, SOUTHERN GULF OF MEXICO

Introduction

To identify disturbance from offshore oil activities, where a host of natural disturbances and long-term variability can produce equivocal evidence of the effects of contamination, suitable designs that consider these factors need to be applied (Clark 1982, Spies 1987). Background information, adequate controls and long-term monitoring, plus a combination of samples taken on a regional basis and along radial gradients around platforms, appears to be the most adequate design for studying marine benthic assemblages and oil-related effects (Carney 1987, Olsgard & Gray 1995, Green & Montagna 1996, Ellis & Schneider 1997, Pearson & Mannvik 1998, Patin 1999). Such an approach has proved successful in the North Sea in monitoring the effects of offshore oil activities (Dicks 1976, Hartley 1984, Daan & Mulder 1995, 1996a, b). The main findings include localised gradients of decreasing disturbance, with severe reduction in fauna close to platforms, a peak in opportunist species 500 to 1000m away and subtle effects up to 2km (Addy *et al.* 1984, Davies *et al.* 1984, Kingston 1987, 1992). Subsequently, effects have been detected up to 6km suggesting that the local approach was no longer suitable (Gray *et al.* 1990, Olsgard & Gray 1995). Taking such a regional approach has identified that the influence of natural variability can be from 6 to 10 times greater in areas affected by oil-related activities than in control sites (Pearson & Mannvik 1998).

In contrast, the experience from the Northern GoM suggests that long-term effects are very localised around the point source (Middleditch 1981a and papers therein, Neff *et al.* 1989, Montagna & Harper 1996). However, major differences exist in relation to studies within the North Sea, such as lack of background information and suitable controls. Additionally, low levels of oil hydrocarbons are spread from natural oil seeps in the Gulf, supplemented possibly by the long history of oil exploitation. Additional natural variability from river runoff, associated anoxia-hypoxia and differences in major natural variables (e.g. depth and grain size) have hindered the identification of generalized effects in the Gulf (Carney 1987, Spies 1987, Green & Montagna 1996). In the southern GoM, no previous attempt has been made to evaluate oil-related influences on benthic infauna (Vazquez *et al.* 2000) and the only available data are from a single survey of a natural seep and the assessment of effects on shrimp populations (Soto & Gracia 1987, Gonzalez-Macias 1989).

The approach adopted for this study is a regional survey that combines a transect design along gradients of the main natural variables and disturbance intensities, also including sites close to active oilfields. The hypothesis to be addressed is that stations within 3km from a given oil field or stations located in areas of high density of oilrigs will exhibit low densities and a different community composition than those further away. The design allows for spatial and temporal changes due to natural disturbance, which would follow similar patterns as those described for shelf environments influenced by river runoff and transitional environments of terrigenous to carbonate sediments. The survey also allows for the fact that effects might extend beyond the immediate area of platform influence; this can be differentiated, as impacted areas tend to show greater variability (Warwick & Clarke 1993b).

Methods

Study site

The area is located in a sector between 19° 00' to 19° 40' latitude North and 91° 40' to 92° 30' longitude West within the muddy transitional environment of the carbonate and terrigenous provinces of the Campeche Bank and Bay (Chapter 1). Details of the sedimentary environment and hydrology have been described previously. Discharges of the Grijalva-Usumacinta and San Pedro-San Pablo rivers, winter storms or "Northers" and intrusion of oceanic water from the Caribbean current are the driving physical processes on the shelf (Monreal-Gomez *et al.* 1992, Salas-de-Leon *et al.* 1992, Vidal *et al.* 1994). The study area includes the largest offshore oil production region in Mexico, covering an area of 8000 km^2 that includes natural oil seeps and approximately 200 platforms with a range of functions. Oil activities in Campeche Bay have developed since 1974 with the discovery of several giant and super giant oil fields (Santiago & Baro 1992). The largest offshore oil-related accident occurred in the Campeche Bay with the Ixtoc I production well blowout in 1979 (IMP 1980, Boehm *et al.* 1982, Botello *et al.* 1982). Subsequently, some relatively minor oil-spills incidents occurred from the Abkatum, Yum and Och fields in 1986, 1987 and 1988 respectively (Lizarraga-Partida *et al.* 1991).

Study design

The classic design for offshore oil-related impact studies consists of a radial disposition of sites from the point source (Middleditch 1981a, Davies *et al.* 1984, Kingston 1987, Neff *et al.* 1989, Daan *et al.* 1992). However, evidence of influences beyond 6km from platforms with a history of exploitation suggested that a wider area should be considered (Gray *et al.* 1990, Kingston 1992, Olsgard & Gray 1995, Pearson & Mannvik 1998).

Considering the long history of oil exploration and production in the southern GoM, plus the numerous platforms that exist at present, it can be expected that platform influences overlap across an extensive area. Hence a regional approach is proposed to investigate its impact on the benthic community, which is the first of its type employed in the southern GoM.

The sampling design consisted of four transects along natural variations of depth, influence of river runoff and depositional environment. Transect A-B followed a depth and sediment gradient from 12 to 135 metres, 40 km NW offshore of the Terminos Lagoon system (Figure 4.1). Transect C-D followed a putative sediment and carbonate content gradient along isobaths ranging from 30 to 50 metres deep, and was situated 60-70 km NNE offshore extending away from the influence of the major rivers. Twelve sites were allocated to each transect at approximately 7 km apart: Each pair of transects transverse the oil activities zone (Figure 4.1). The separation of stations was chosen to represent the regional variation within the transitional sedimentary environment. Nevertheless, the situation of the transects allowed for a more intense sampling in the area of high platform densities in order to detect potential overlapping influences on the benthos. A total of 15 stations were located between 1 and 3 km from a number of platforms, (this is a distance where effects have been detected in areas of the North Sea); 12 stations had between 4–12 oil rigs within a 5 km radius from the site. Thus, the present design is unique in the fact that it is not considering effects from a point source (as traditional designs have previously done), but rather putative effects on a greater scale of influence. The approach intends to compensate for the long history of exploitation and make comparisons within the context of natural disturbance from river runoff and winter storms in the area (Chapter 3).

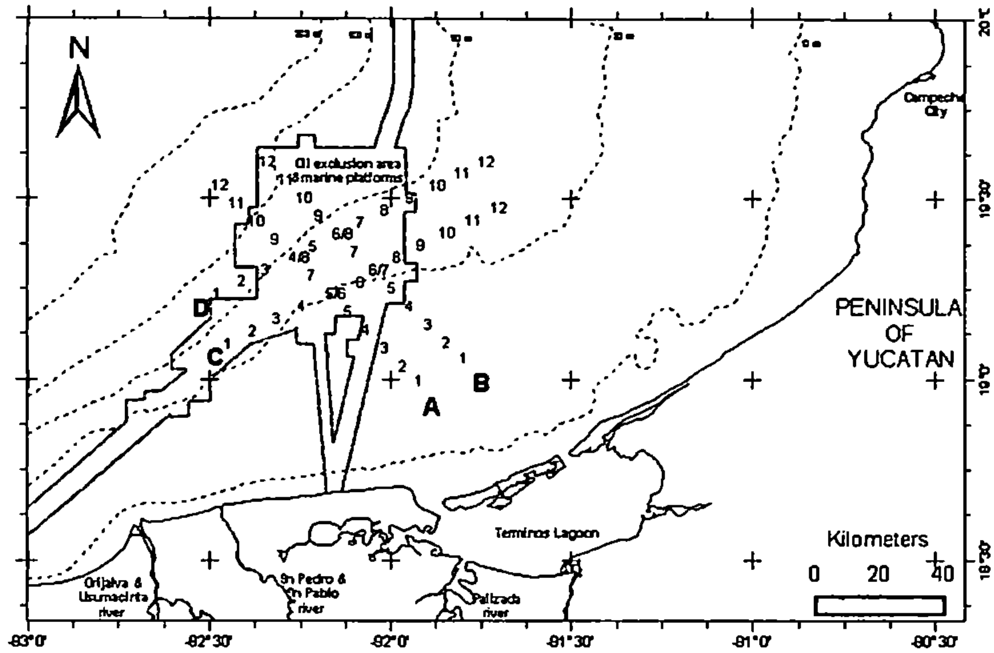


Figure 4.1 Study area showing the location of stations along the four transects A-D. Stations were sampled for superficial sediments in November 1999 (after the rainy season) and April 2000 (after the northers season). Transects A-B followed a depth gradient and C-D followed a putative sediment gradient.

Sampling methodology

Sampling was carried out from 11th - 13th November 1999 after the rainy season and from 14th – 16th April 2000 after the "northers" season and at the beginning of the dry season. Sites were located and positioned using the satellite navigation system of the vessel and sampled without replication using a box corer. The recovered core was sub-sampled on board and the description of the sampling of natural variables and fauna is given in chapter 3. Sub-Samples for oil hydrocarbons and trace metals were taken using a Teflon^{TM} core of 15 cm in diameter to a depth of 5 cm, which was then transferred to a high-density polyethylene plastic pot, labelled and frozen until analysis.

Laboratory analyses

Details of the methodology for macroinfauna and natural variables analysis can be found in the methods section of Chapter 3 . Concentrations of Iron, Manganese, Zinc, Copper, Nickel, Chromium and Barium were quantified by Induction Coupling to Plasma emission spectroscopy. Dried samples were digested with hydrochloric acid at 5% to extract the bio-available fraction of metals, or those that are contained in the organic matter and soluble sediments. Hydrocarbon analyses were undertaken using soxhlet extraction for 12 hours into dichlorometane, followed by clean up and fractionation through a silica/alumina gel column chromatography (Sericano *et al.* 1990, UNEP/IOC/IAEA 1992). The individual aliphatic (n-C10 to n-C34, pristane and phytane) and aromatic hydrocarbons (22 compounds) were identified and quantified by high-resolution gas chromatography (GC) using a Hewlett Packard HP5890 series II with a flame ionisation detector (FID). The measure of total aliphatic and aromatic hydrocarbons includes all resolved peaks and the area covered by the unresolved complex mixture. To assure quality control appropriate blanks and reference materials were analysed simultaneously with each batch of samples.

Data analyses

Univariate approach. Simple graphs of concentrations of total oil hydrocarbons, metals and biological measures (see Chapter 3 for number of families and individuals, biomass and Shannon-Wiener diversity index Log_e plots) along transects for each fraction/season were constructed in order to identify spatial patterns of distribution. To test the hypothesis that stations located in areas of high density of oil rigs present lower values of biological measures, stations were classified in relation to the number of oil rigs within a radius of 5 km: high density (4-12), low density (1-3) and no oil rigs. A two factor ANOVA balanced design was applied to test for differences in mean values of number of individuals and biomass between season (NB similar to the ANOVA analysis in Chapter 2, the factor season refers to differences between sampling dates and not to multiyear seasonal variations) and among densities of oil rigs for a randomly selected subsets of 11 stations for each density (see Appendix 5 for selected stations). This was followed by multiple linear regression analysis to estimate and fit a structural model to explain the variation in the observations of biological measures in terms of natural variables and concentrations of oil hydrocarbons and metals. The analysis is an extension of that carried out using only natural variables (Chapter 3), the rationale being that if variability of biological measures are best explained by natural variables, these would remain the best-fit variables selected from a suite of natural and anthropogenic measures. Variables were checked for colinearity using the Pearson's product moment correlation coefficients. Where a combined coefficient for a pair of variables was above 0.95 and significant at 5% confidence level, one variable was not included in the regression analysis. Thus the resulting selected variables were depth, mean grain size, % silt, sorting, organic matter, total hydrocarbons, iron, barium, chromium and nickel. All variables were checked for normality using the Wilk's λ and transformed when necessary either with $\log_{10}$ for continuous measurements or arc-sin transformation for variables expressed as a percentage.

Graphical/distributional methods. Abundance-Biomass Comparison (ABC) curves (Warwick 1986, Warwick & Clarke 1994) were run for each site/season using the combined matrices for small and large maroinfauna expressed per square metre. The pooling of the two fractions allowed correct representation of the large fauna that is often underestimated because of small sample sizes. The ABC method has been considered suitable to identify impacted communities without reference to spatial or temporal controls (Beukema 1988, McManus & Pauly 1990), where in undisturbed assemblages the biomass curves will always lay above the abundance curve and conversely for disturbed conditions. However, due to the large number of stations, an alternative presentation of results was used, namely the W statistic (for details see Clarke 1990). The W statistic summarises in a single value the configuration of the Abundance-Biomass plot. Its value ranges from +1 to −1 where undisturbed or unpolluted sites have positive values of W and disturbed or polluted sites have negative values of W.

Multivariate approach. Multivariate analysis was undertaken by utilising the PRIMER (Plymouth Routines in Multivariate Ecological Research) package (for details see Clarke 1993, Clarke & Warwick 1994, Clarke & Gorley 2001). The sets of 23 environmental variables (natural and anthropogenic) from each season were subjected to Principal Component Analysis (PCA) on a normalised correlation matrix after suitable transformation. (Arcsin transformation for variables expressed as percentages (Sokal & Rohlf 1995) and Log_{10} for the remaining variables except depth and distance to oilfields which remained untransformed).

Faunal analyses. Non-metric multidimensional scaling (MDS) ordination plots were produced using a ranked similarity matrix, based on Bray-Curtis similarity measures of fourth root transformed macroinfauna family abundance and biomass data for each fraction/season (Chapter 3). The relationship between community composition and environmental variables was examined by scaled superimposition of selected anthropogenic variables on the ordination plots of abundance data. Following previous studies of offshore oil related effects, the sampled sites were grouped based on distance to the nearest oilfield: stations <3km where severe effects are expected, stations likely to show moderate to subtle influence within 3-8km and finally all sites beyond 8km, which are expected not to be influenced by oil-related activities. This *a priori* grouping provides the model to be formally tested by means of a one-way ANOSIM (Clarke & Green 1988, Clarke 1993) hypothesising no spatial differences in community composition with distance to oilfields on an unbalanced design. An *a posteriori* criterion was set based on concentrations of barium in sediment as an indicator of drilling activities. Three groups of sites with <100 mg/g, 100-200 mg/g and >200mg/g of barium in dry sediment were used as a proxy of the influence of oil related activities influence and the formal test of no differences in community composition was performed.

The relationship between community composition and environmental variables was examined by superimposition of the selected environmental variables and more objectively by the BIOENV procedure (Clarke & Ainsworth 1993). BIOENV uses a Spearman's Rank Correlation between the resulting ranked similarity matrices of fauna and correlation-based PCA of the normalised environmental variables. Variables were checked for co-correlation and those with a coefficient of 0.95 or higher were removed, hence the analysis was run on a data set of 10 variables.

Multivariate measures of community stress. The following three methodologies have been recently devised and their use is considered more as a validation of their utility in tropical environments rather than objectively generalised methodologies (Clarke & Warwick 1994).

The meta-analysis procedure was used to compare the severity of community stress between the Southern GoM and a training data set from the NE Atlantic that considers various types of disturbances (Warwick and Clarke, 1993a). It comprises standardised approximate measures of Production (P) at phylum level from the allometric equation

P=(biomass/abundance)$^{0.73}$ x abundance. Thus, abundance and biomass data from the Campeche Bay were aggregated to phylum, combined to form the production matrix using the above formula, standardised and merged into the original database. Finally an MDS was performed on 4th root transformed data using the Bray-Curtis similarity index.

Warwick & Clarke (1993b) proposed that variability in community composition increases with increased levels of stress. The Index of Multivariate Dispersion (IMD) and the relative dispersion of the groups set with the criteria of distance to oilfields and barium concentrations based on the similarity matrices were calculated to explore the above proposition.

In Chapter 3 it was noted that zonation patterns have been identified across continental shelves in relation to depth and sedimentation gradients. However, this zonation pattern is perhaps better described by a sequential pattern of community change termed 'seriation' (Clarke *et al.* 1993). This pattern of seriation can be altered by disturbance, and the Index of Multivariate Seriation (IMS) can measure this alteration. The IMS is defined as a Spearman rank correlation coefficient calculated between the triangular matrices of dissimilarities of transformed abundance for all pairs of samples from each fraction/season/transect and the inter-point distances of n points laid out, equally spaced along a line (for details of the technique see Clarke *et al.* 1993, Clarke & Warwick 1994, Clarke & Gorley 2001). The IMS takes values of 1 when the community changes exactly match the ranking in the linear sequence, and approaches to zero when there is no discernible biotic linear pattern along the transect. A statistical significance test using a Monte Carlo permutation procedure is then used to test the null hypothesis of total absence of seriation (i.e. there is not a linear sequence of change in community composition along the transects in relation to depth or moving away from the rivers influence). The presence of seriation will support the assumption that changes in community composition along the transects are due to natural variability, however, the absence of seriation will imply that oil-related activities are causing the breakdown of seriation.

Results

Univariate analyses

Indicators of oil-related activities along the depth gradient were present in low concentrations at stations 1 to 4; these stations are located in an area with no oil-related activities. Total hydrocarbons and barium were below 20 µg/g and 40 µg/g of dry sediment respectively and in general these stations had the lowest concentrations of metals (Figure 4.2). Total hydrocarbons, barium and chromium peaked in their concentrations at sites closer than 5 km from the nearest oilfield. Along transects C-D total hydrocarbons, barium, chromium and nickel all showed an erratic pattern, although with peaks at stations close to oilfields (Figure 4.2). In contrast, metals more likely to have a terrigenous source (e.g. Iron) showed a depth-related gradient and a decreasing pattern from SW to SE moving away from the rivers' influence (Figure 4.2). This pattern resembles that of sediment size along the depth gradient and is inverse to the carbonate gradient along transects C-D, indicating a dilution of carbonaceous material by terrigenous sedimentation.

Table 4.1 presents the results from the two factors ANOVA. The null hypothesis of no differences in mean density and biomass between seasons and among density of oil rigs was rejected. For the small macroinfauna, significant differences occurred between seasons and among densities of oil rigs. The lowest mean densities and biomass were present during the rainy season (November 1999) and for the high rig-density group of stations. For the large macroinfauna, significant differences were also present between seasons and among densities of oil rigs but only for the abundance data, with a lower abundance during the rainy season and for the high rig-density group. It was evident that stations located in areas of high oil rig density (i.e. within a 5 km radius) had a low abundance and biomass compared to those with zero oil rigs in the vicinity. However, SNK test showed that there were no significant differences between the high and low density of oilrigs groups, although the mean value for the high-density group was always lower.

Table 4.1. Two factor fixed-orthogonal ANOVA model testing for differences and interactions in macrobenthos abundance and biomass between two seasons (Rainy and 'northers;) and three densities of oil rigs (high, low and zero oil rigs within a 5 km radius). To remove heterogeneity in the variances of abundance and biomass, data were log (x+1) transformed.

Small macroinfauna

Factor	SS	d.f.	MS	F	P
Number of individuals					
Season	11.2553	1	11.2553	12.95	**0.0006**
Density of rigs	9.1216	2	4.5608	5.25	**0.0079**
Season x density of rigs	0.8256	2	0.4128	0.48	0.6242
Residual	52.1417	60	0.8690		
Total	73.3443	65			
Biomass					
Season	8.3377	1	8.3377	6.12	**0.0162**
Density of rigs	9.9342	2	4.9671	3.65	**0.0320**
Season x density of rigs	0.1605	2	0.0802	0.06	0.9428
Residual	81.6905	60	1.3615		
Total	100.1228	65			

Large macroinfauna

Factor	SS	d.f.	MS	F	P
Number of individuals					
Season	15.9052	1	15.9052	18.79	**0.0001**
Density of rigs	14.4437	2	7.2218	8.53	**0.0005**
Season x density of rigs	1.5787	2	0.7893	0.93	0.3992
Residual	50.7832	60	0.8464		
Total	82.7108	65			
Biomass					
Season	0.0007	1	0.0007	0.00	0.9774
Density of rigs	3.9742	2	1.9871	2.33	0.1061
Season x density of rigs	1.4499	2	0.7250	0.85	0.4325
Residual	51.1728	60	0.8529		
Total	56.5975	65			

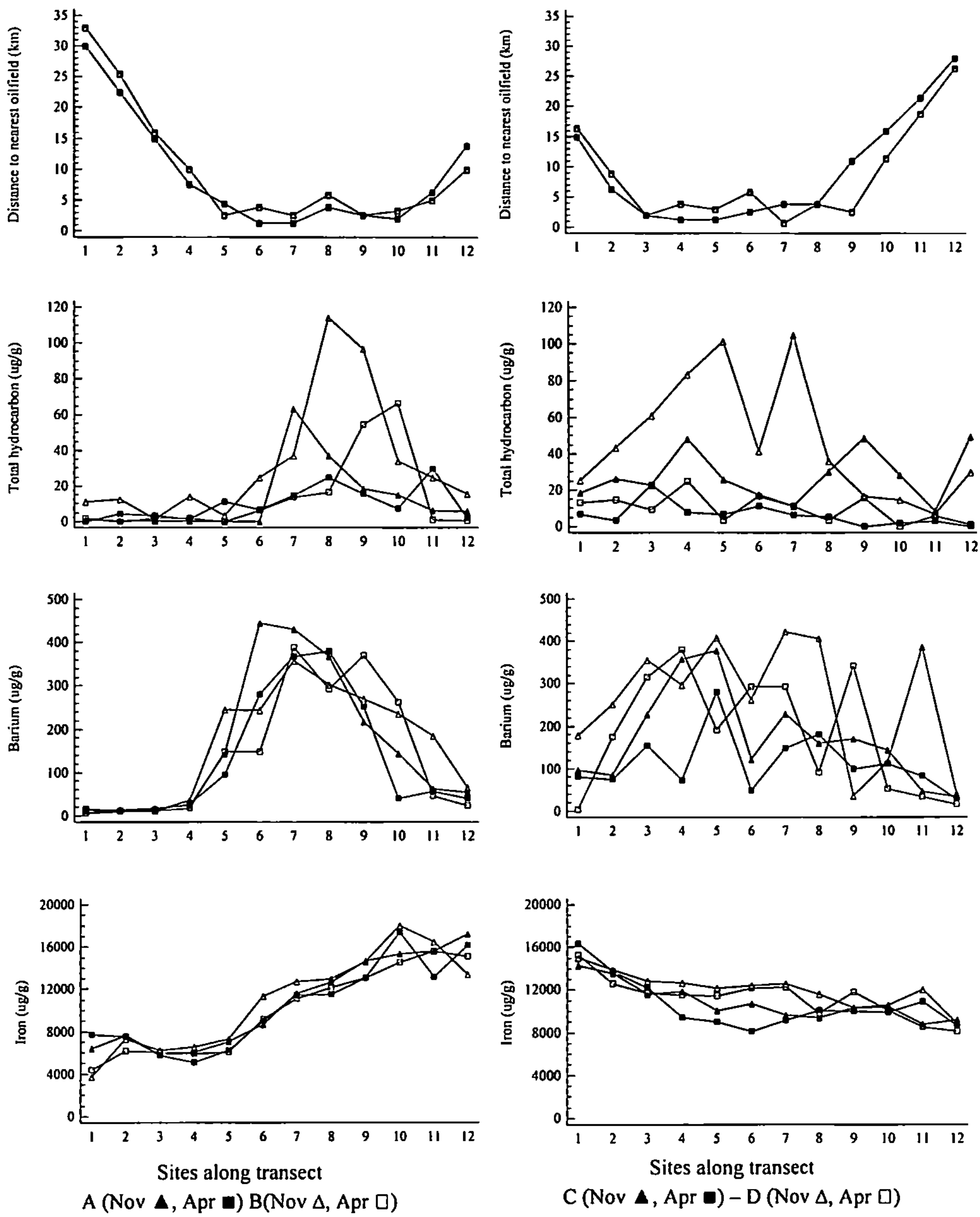


Figure 4.2. Patterns of variables indicative of oil related activity measured at each site along transects A to D. Lines are as an aid to follow each transect.

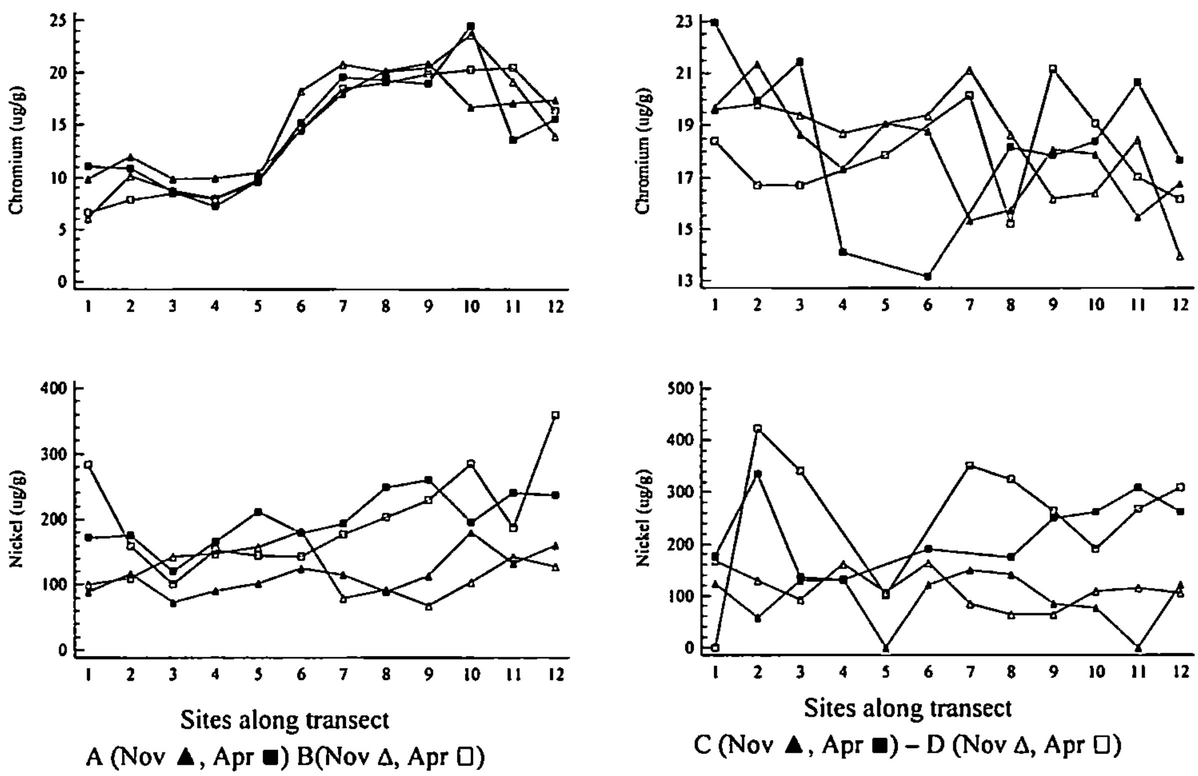


Figure 4.2 continued. Patterns of variables indicative of oil related activity measured at each site along transects A to D. Lines are as an aid to follow each transect.

Multiple linear regression analysis

Table 4.2 presents the best-fit models (statistically significant at $p<0.05$) in explaining the highest amount of variation in number of taxa, $\log_{10}$ (number of individuals) and $\log_{10}$ (biomass) in terms of five natural and five anthropogenic variables transformed.

Small macroinfauna: along transects A-B the best explanatory variables changed with season. During November 1999 (Table 4.2a) 57% and 50% of the total variation in number of taxa and number of individuals respectively was explained solely by concentrations of barium in the sediment (Figure 4.3). During April 2000 (Table 4.2b), however, the organic matter content explained 25% of variation in number of individuals and biomass respectively. Along transects C-D the explanatory variables also varied with season. During November 1999 (Table 4.1a) percentage of silt explained above 30% of the variation in number of taxa and number of individuals respectively. During April, number of individuals presented a relationship with depth that explained 29% of variation, although the p-value of the constant was not significant (Table 4.2b). No relationship was found with biomass.

Large macroinfauna: along transects A-B during November 1999 (Table 4.2a), a combination of mean grain size, barium and nickel best explained the variation in number of taxa (86% of variability); the variation in number of individuals (74%) was explained mostly by mean grain size and barium (Figure 4.3). However, mean grain size alone best explained the variation in biomass (59%). During April 2000, the explanatory variables varied with type of biological measure. For example, chromium explained 51% of variation in number of taxa; mean grain explained 68% of variability in number of individuals and 46% of variation in biomass was best explained by depth (Table 4.2b). Along transect C-D the explanatory variables also changed with type of biological measure and season. During November 1999 (Table 4.2a), sediment sorting and barium explained 52% of variation in number of taxa. Barium explained 35% of variability for number of individuals (Figure 4.3) and sorting, iron, chromium and nickel explained 65% of variation in biomass. During April 2000 (Table 4.2b) percentage of silt and iron explained 47% of the total variation in number of taxa, barium and nickel explained 29% of variation in number of individuals (Figure 4.3) and organic matter explained 30% of variation in biomass.

Table 4.2a. Models from stepwise multiple linear regression analysis that best explain variation in the observations of number of taxa, log_{10} number of individuals, log_{10} Biomass; for each fraction in Nov 99 along transects A-B and C-D.

November-99 small macroinfauna transects A-B (n=22)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	19.1746	<0.0001	2.2315	<0.0001		
Barium	-5.4520	<0.0001	-0.5969	0.0002	**None**	
Regression		<0.0001		0.0002		
R-square	0.5758		0.5073			

November-99 small macroinfauna transects C-D (n=24)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	70.1262	0.0012	11.7943	0.0011		
% Silt	-1.1207	0.0026	-0.1726	0.0047	**None**	
Regression		0.0026		0.0047		
R-square	0.3439		0.3102			

November-99 large macroinfauna transects A-B (n=24)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	59.3186	<0.0001	3.6740	<0.0001	3.8617	0.0001
MGS	-3.0414	0.0002	-0.2979	0.0009	-0.6795	<0.0001
Barium	-5.4889	<0.0001	-0.4153	0.0023		
Nickel	-10.2568	0.0269				
Regression		<0.0001		<0.0001		<0.0001
R-square	0.8666		0.7452		0.5994	

November-99 large macroinfauna transects C-D (n=24)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	-7.5981	0.4370	1.9959	<0.0001	9.2890	0.0007
Sorting	13.3866	0.0085			1.0270	0.0009
Barium	-4.4419	0.0105	-0.5228	0.0022		
Iron					-3.7069	0.0006
Chromium					3.0611	0.0302
Nickel					0.1910	0.0023
Regression		0.0004		0.0022		0.0001
R-square	0.5283		0.3523		0.6957	

Table 4.2b. Models from stepwise multiple linear regression analysis that best explain variation in the observations of number of taxa, log_{10} number of individuals, log_{10} Biomass; for each fraction in April 00 along transects A-B and C-D.

April 00 small macroinfauna transects A-B (n=22)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant			1.9546	<0.0001	-0.8667	0.0030
Organic matter			-0.1468	0.0139	-0.1604	0.1600
Regression				0.0139		
R-square			0.2663		0.2572	

April 00 small macroinfauna transects C-D (n=22)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant			-2.1286	0.1030		
Depth			2.0373	0.0160	**None**	
Regression				0.0160		
R-square			0.2819			

April 00 large macroinfauna transects A-B (n=22)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	64.3997	<0.0001	4.7123	<0.0001	2.0221	0.0007
Chromium	-41.8171	0.0001				
MGS			-0.4656	<0.0001		
Depth					-1.3839	0.0003
Regression		0.0001		<0.0001		0.0003
R-square	0.5154		0.6894		0.4692	

April 00 large macroinfauna transects C-D (n=22)

Predictor	Number of taxa		Number of individuals		Biomass	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Constant	139.168	0.0010	1.4873	<0.0001	1.7492	0.0228
Silt	-0.7449	0.0220				
Iron	-21.4289	0.0199				
Barium			-0.4464	<0.0001		
Nickel			0.2933	0.0004		
Organic matter					-0.4015	0.0121
Regression		0.0041		0.0001		0.0121
R-square	0.4756		0.6715		0.3021	

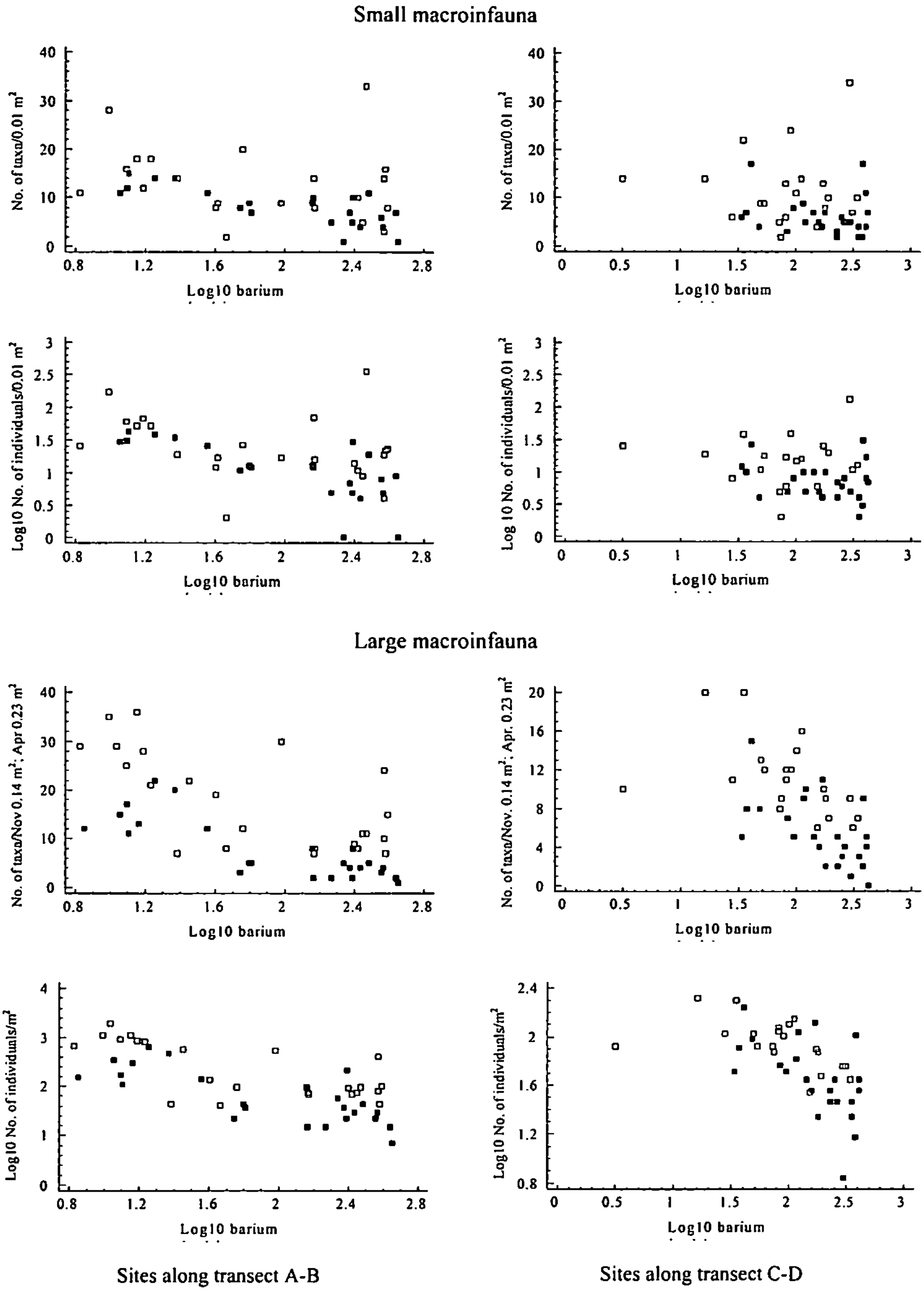


Figure 4.3. Scatterplots of small and large macroinfaunal biological measures against concentrations of $\log_{10}$-barium along transects during November 1999(▪) and April 2000 (□).

Abundance-Biomass Comparison

Results showed an inconsistent pattern of disturbance according to season. During November 1999 two stations along transect A and three stations along transect B presented the disturbed pattern with the abundance curve above the biomass curve i.e. negative value of the W statistic (Figure 4.4). Along transects C-D the number of 'disturbed' stations was two at each transect. During April 2000, the number of disturbed stations increased along all transects except at transect D, although the disturbed stations were inconsistent from one season to another. The spatial distribution of the putatively polluted stations was not restricted towards the crossing of transects: For example, stations from the inner shelf where no oilrigs are present showed a disturbed pattern, particularly during April, four months after the end of the rainy season (Figure 4.4). The overall lack of consistency in relation to the disturbed or polluted status of the stations is clear.

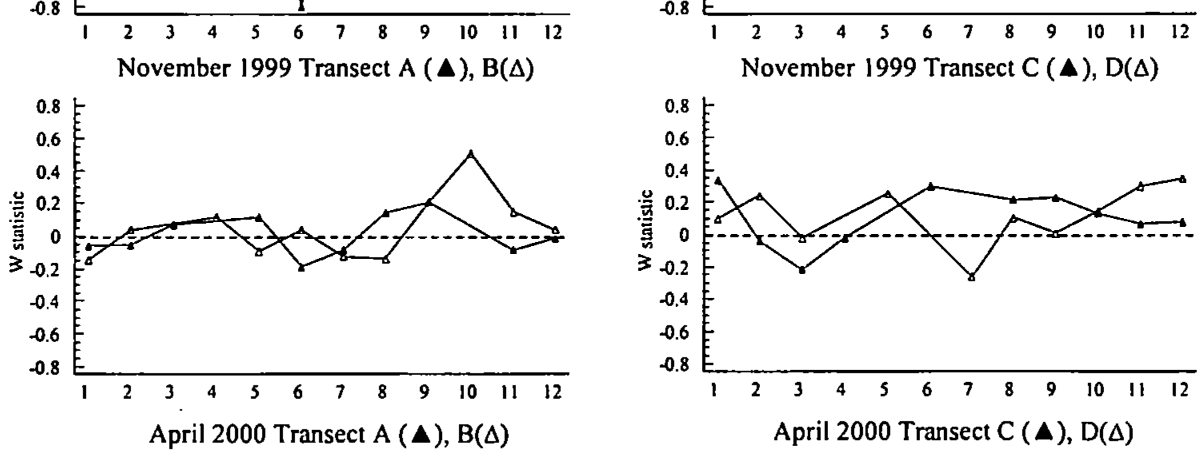


Figure 4.4. Values of W-statistic to summarise the pollution status of stations along each transect for each season. Combined biomass and abundance data for both small and large macroinfauna were used, standardised per square metre. Negative values represent disturbed stations where the abundance curve runs above the biomass curve (see text).

Multivariate analyses

Principal Components Analysis (PCA): The physical and chemical features of the sampled stations are summarised by the PCA of the 23 measured variables including indicators of anthropogenic influence (Figure 4.5). The PC1 explains 55 % of variation in November and April respectively and relates to increasing (November) and decreasing (April) values from left to right of sediment parameters, metals load and organic matter, followed by a weaker contribution of oil hydrocarbons, barium and depth (Table 4.3). The second PC axis explains 12 and 15% of variation respectively and during November is dominated by silt and oil hydrocarbons that decrease in magnitude from bottom to top. In April, depth is the most dominant variable decreasing from bottom to top followed by sediment parameters, distance to oilfields and zinc (Table 4.3). A change in the general layout of stations can be observed when compared with the ordination plots using only natural variables, which followed a more linear pattern according to depth (Figure 3.9). However, when metals and hydrocarbons are included in the ordination the linear pattern from shallow to deep sites appears to be broken along PC1.

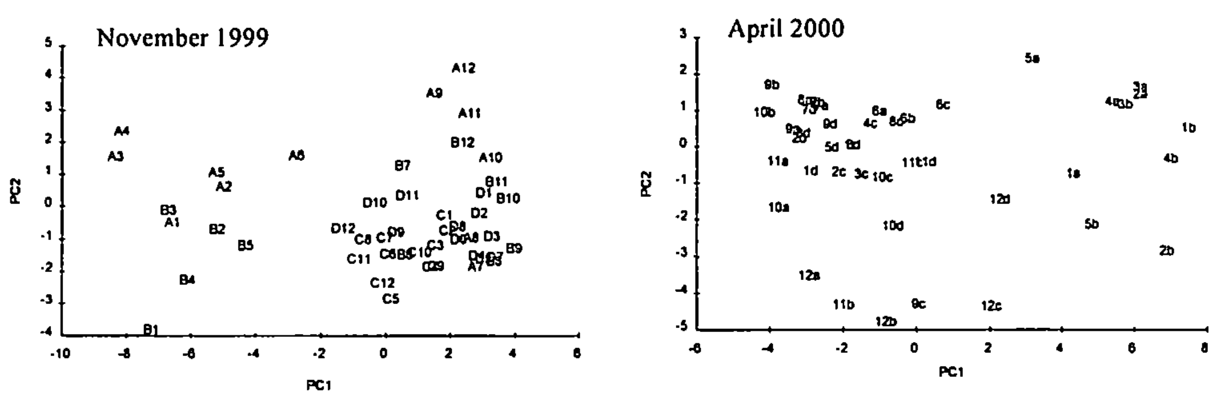


Figure 4.5. PCA ordination plot of the first two PC for 23 transformed environmental variables by season. Compare with Figure 9 from chapter 3 when only natural variables are included.

Table 4.3. Eigenvalues, percentage of variation explained and coefficients for the linear combination of 23 variables making up the first two PC for 48 and 44 stations sampled during November 1999 and April 2000 respectively. Bold figures are coefficients of the most influential variables.

	November 1999		April 2000	
	PC1	**PC2**	**PC1**	**PC2**
Eingenvalues	12.81	2.81	12.43	3.56
% of variation	55.7	12.2	54.1	15.5
Variable/coefficients				
Depth m	0.167	**0.353**	-0.168	**-0.242**
Oil fields km	-0.139	-0.066	0.17	-0.161
log salinity	0.226	0.113	0.145	0.111
Asin Sand	-0.203	0.155	**0.255**	0.054
Asin Silt	0.1	**-0.336**	-0.146	0.037
Asin Clay	**0.247**	0.163	**-0.256**	-0.174
Log Surface area (m2 gm-1)	**0.239**	0.104	**-0.262**	-0.144
Moment mean (phi)	**0.25**	-0.006	**-0.264**	-0.133
Moment stdev.(phi)	-0.092	**0.337**	0.167	-0.017
Asin organic matter	0.209	0	**-0.255**	-0.083
Asin carbonates	-0.235	-0.2	**0.244**	0.099
Log Total-Hydrocarbons	0.212	**-0.285**	-0.168	**0.401**
Log Total Aliphatic	0.192	**-0.327**	-0.154	**0.382**
Log Total aromatic	0.197	-0.217	-0.161	**0.367**
Log UCM aliphatic	0.193	**-0.327**	-0.145	**0.385**
Log UCM aromatic	0.205	-0.215	-0.16	**0.369**
Log [iron]	**0.26**	0.18	**-0.257**	-0.122
Log [manganese]	**0.251**	0.2	**-0.261**	-0.086
Log [zinc]	**0.254**	0.193	-0.235	-0.146
Log [copper]	**0.247**	0.072	**-0.261**	-0.094
Log [chrome]	**0.256**	0.039	**-0.249**	-0.083
Log [barium]	0.202	-0.048	-0.186	0.166
Log [nickel]	0.007	0.15	0.002	-0.013

Non-Metric Multidimensional Scaling: Figures 4.6-4.9 present the 2-d MDS ordination plots for transformed abundance data for each fraction/season (as presented in figures 3.10-3.13). Two grouping criteria have been displayed: a) distance to oil fields and b) concentrations of barium in sediment. For the small macroinfauna, stations at 0-3 km from a given oilfield, and thus with high levels of barium in sediment, are spread at the outer edge of the plot and represent the most impoverished stations. Stations further away from the oil fields and with lower levels of barium are more closely clustered, particularly stations from the inner shelf. For the large macroinfauna, the ordination plot from April provides a more clear pattern, with stations close to a given oilfield and with high levels of barium separating out from other stations. As with the previous plots, impoverished sites are spread around the external edge (being highly dissimilar since they have few taxa in common) and sites from the inner shelf are clustered together. MDS plots for biomass data provided the same information and are not shown.

Analysis of Similarities: The one-way ANOSIM test for differences among groups based on distance to the nearest oil field showed globally significant differences for each season/fraction analysed (Table 4.4), although the global R was relatively small. Pairwise comparison for the small macroinfauna indicated significant differences only between the 0-3 km and the >8 km groups. However, for the large macroinfauna, significant differences extended between the >8 km versus the 3-8 km and 0-3 km group. In contrast, results from the one-way ANOSIM among groups classified in terms of concentration of barium in the sediment only presented global significant differences for the large macrofauna. Pairwise comparison indicated significant differences between the lowest vs. highest and lowest vs. intermediate concentration groups in November and between the lowest and intermediate concentration group in April (Table 4.4).

Linking environmental variables to the multivariate pattern

The superimposition of indicators of river influence and oil-related activities showed no pattern on the MDS plots during either season for neither the small or the large macroinfauna during November 1999 (Figure 4.6-4.8). In contrast the MDS configurations of the large macroinfauna for April 2000 showed an association with iron, distance to oil fields and barium concentrations (Figure 4.9).

Table 4.4. One-way ANOSIM test for differences in community composition among groups based on distance to the nearest oilfield and concentrations of barium in sediment (low <100 µg/g, medium 100-200 µg/g, and high >200 µg/g in dry sediment) for each fraction/season. Statistical significant values are in bold.

	November small macroinfauna		November large macroinfauna		April small macroinfauna		April large macroinfauna	
	R	SL%	R	SL%	R	SL%	R	SL%
Dist. oilfields								
Global	**0.097**	0.7	**0.148**	0.1	**0.112**	1.2	**0.174**	0.2
Pairwise								
>8km, 3-8km	0.002	48.9	**0.154**	0.5	0.12	5.5	**0.131**	3.2
>8km, 0-3km	**0.224**	0.1	**0.2**	0.1	**0.192**	0.2	**0.271**	0.1
3-8km, 0-3km	0.057	11.7	0.069	11.7	-0.033	65.9	0.095	6.5
Barium conc.								
Global	-0.032	75.2	**0.17**	0.3	-0.009	52.7	**0.151**	1.9
Pairwise								
Low, medium	0.05	23.9	**0.161**	2.7	0.008	42.7	**0.204**	1.9
Low, high	0.013	37	**0.23**	0.1	-0.012	50.6	0.142	9.4
Medium, high	-0.131	96.3	0.079	17.2	-0.043	68.2	0.007	42.8

Table 4.5. Relationship between environmental variables and fauna using BIOENV procedure. The combinations of one to five variables that best explain the faunal patterns are given for each fraction/season. The correlation coefficient (r_s) is for Spearman rank correlation. Highest coefficients are in bold. (TH total hydrocarbons)

Nov. small macrofauna		Nov. large macrofauna		April small macrofauna		April large macrofauna	
Variables	r_s	Variables	r_s	Variables	r_s	Variables	r_s
Depth, Sorting, TH, Nickel	0.205	Depth, Organic matter, Iron, Barium	0.239	Depth, Iron, Barium, Nickel	0.184	Depth, Organic matter, TH, Iron	0.426
Depth, Silt, Nickel	0.191	Depth, Organic matter, Barium	**0.255**	Depth, Iron, Nickel	0.241	Depth, Organic matter, TH	0.444
Depth, Nickel	**0.220**	Depth, Barium	0.253	Depth, Iron	0.246	Depth, organic matter	**0.472**
Nickel	0.178	Depth	0.237	Depth	**0.253**	Depth	0.445

BIOENV analysis: Spearman rank correlation between the similarity matrices of fauna and PCA ordinations of a set of 10 variables using the BIOENV technique gave low coefficients (r<0.25) for all data from November and also for the small macrofauna of April (Table 4.5). Depth was the best single explanatory variable for the multivariate configuration of abundance data, except for small macroinfauna during November. The highest coefficient (r=0.472) occurred for the large macrofauna from April with a combination of depth and organic carbon.

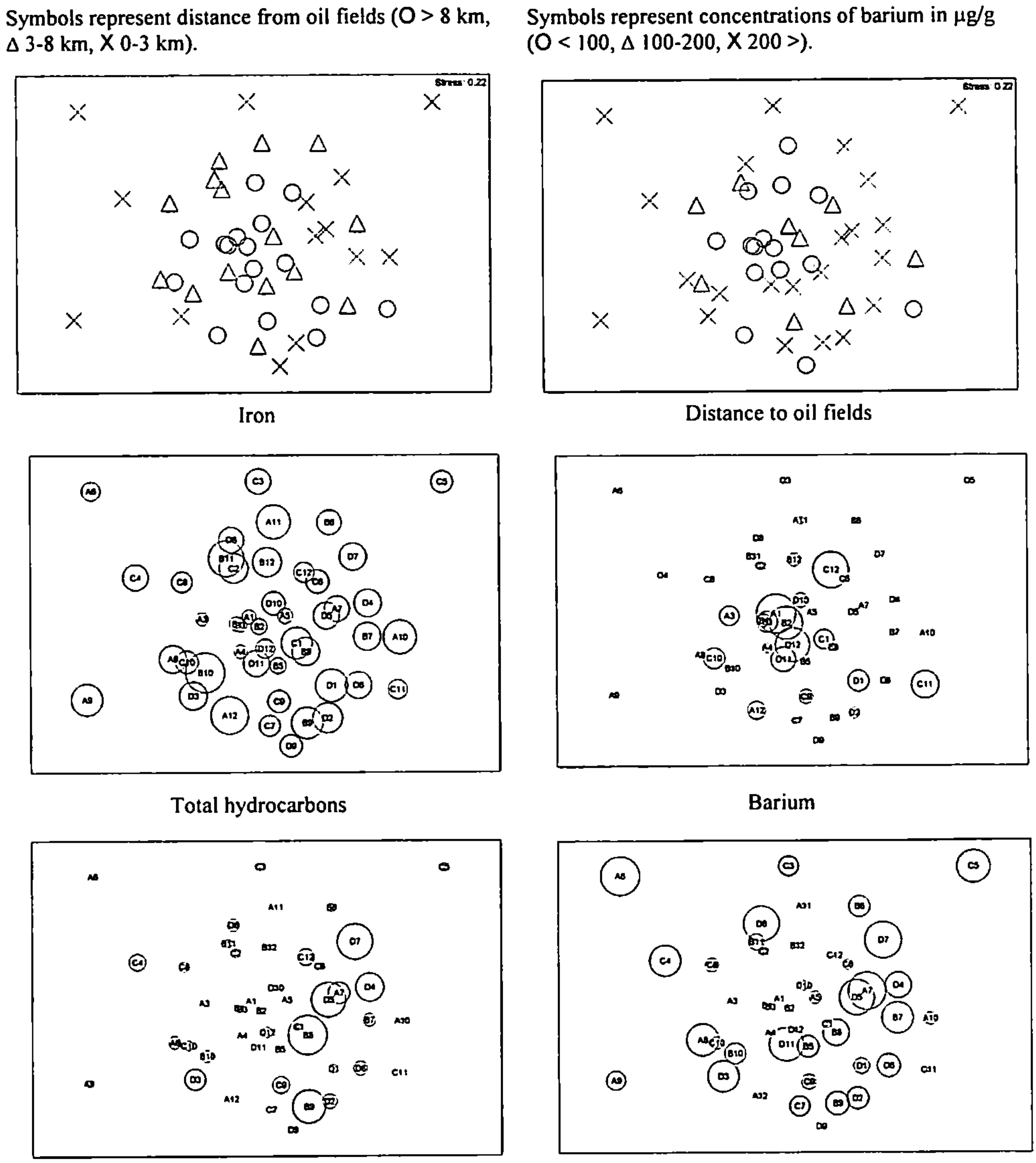


Figure 4.6. 2-d MDS ordination plots assemblage data for small macroinfauna during November 1999 based on Bray-Curtis similarities of abundance (fourth root transformed). Selected indicators of anthropogenic disturbance are superimposed on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

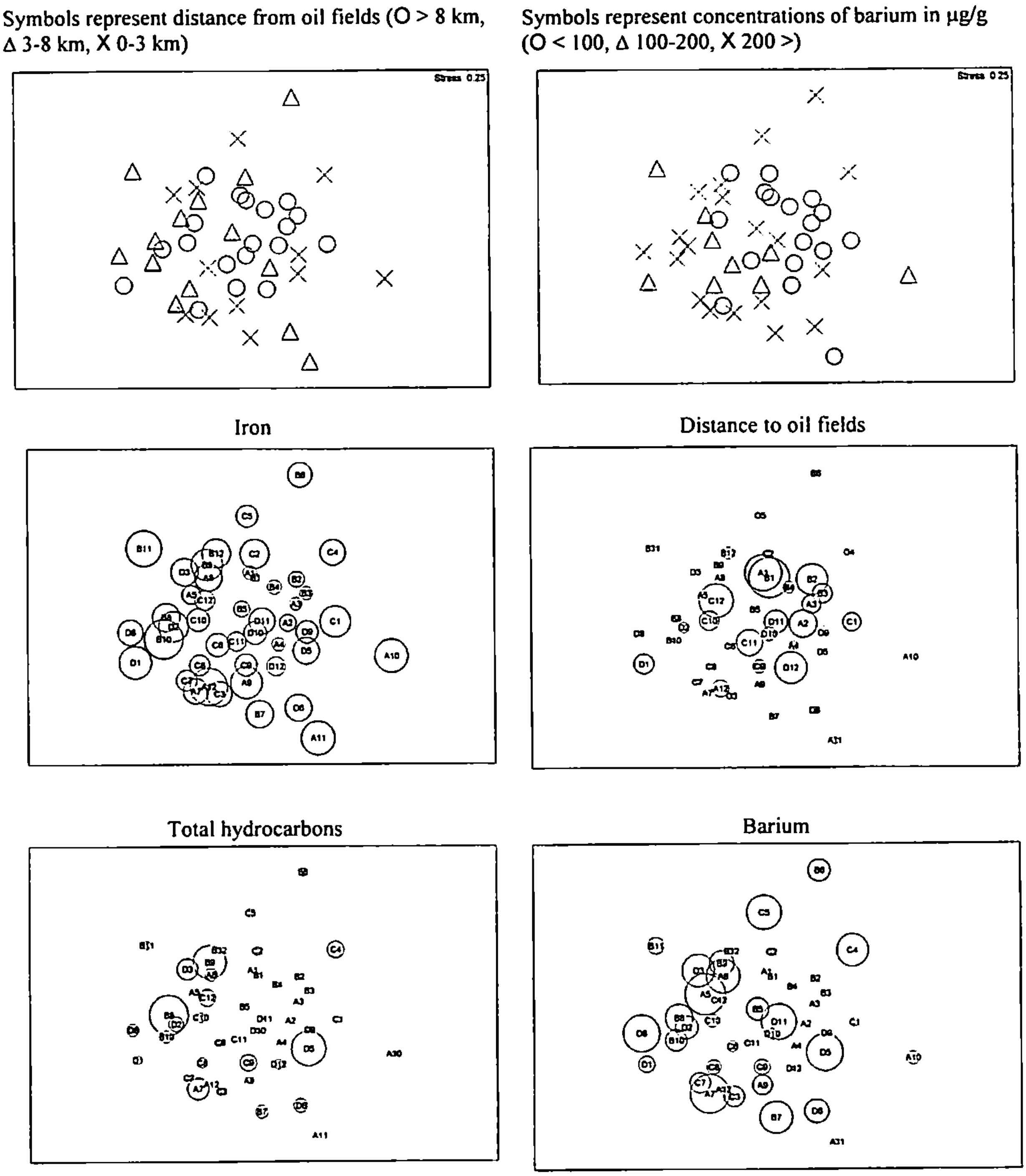


Figure 4.7. 2-d MDS ordination plots assemblage data for large macroinfauna during November 1999 based on Bray-Curtis similarities of abundance (fourth root transformed). Selected indicators of anthropogenic disturbance are superimposed on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

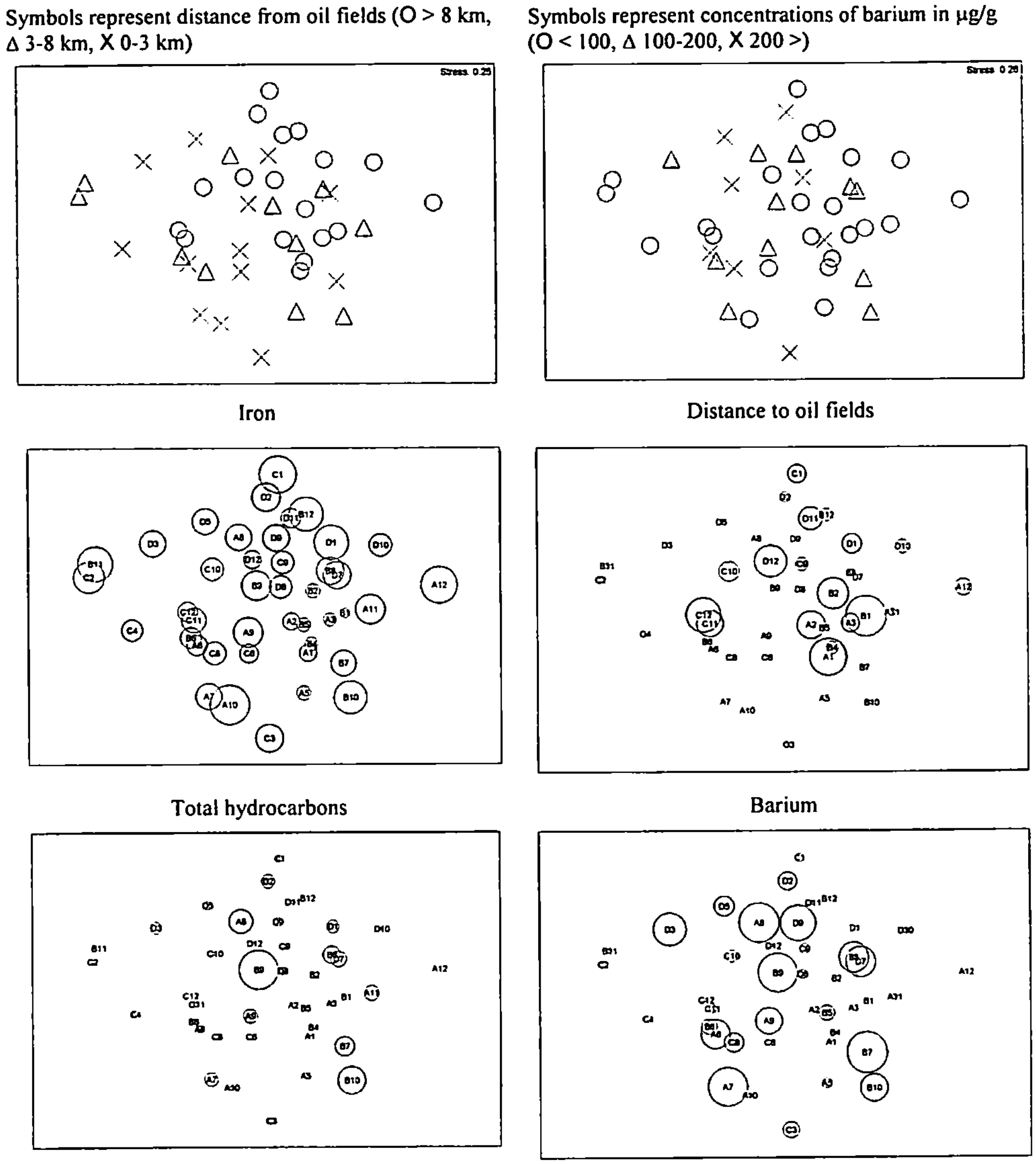


Figure 4.8. 2-d MDS ordination plots assemblage data for small macroinfauna during April 2000 based on Bray-Curtis similarities of abundance (fourth root transformed). Selected indicators of anthropogenic disturbance are superimposed on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

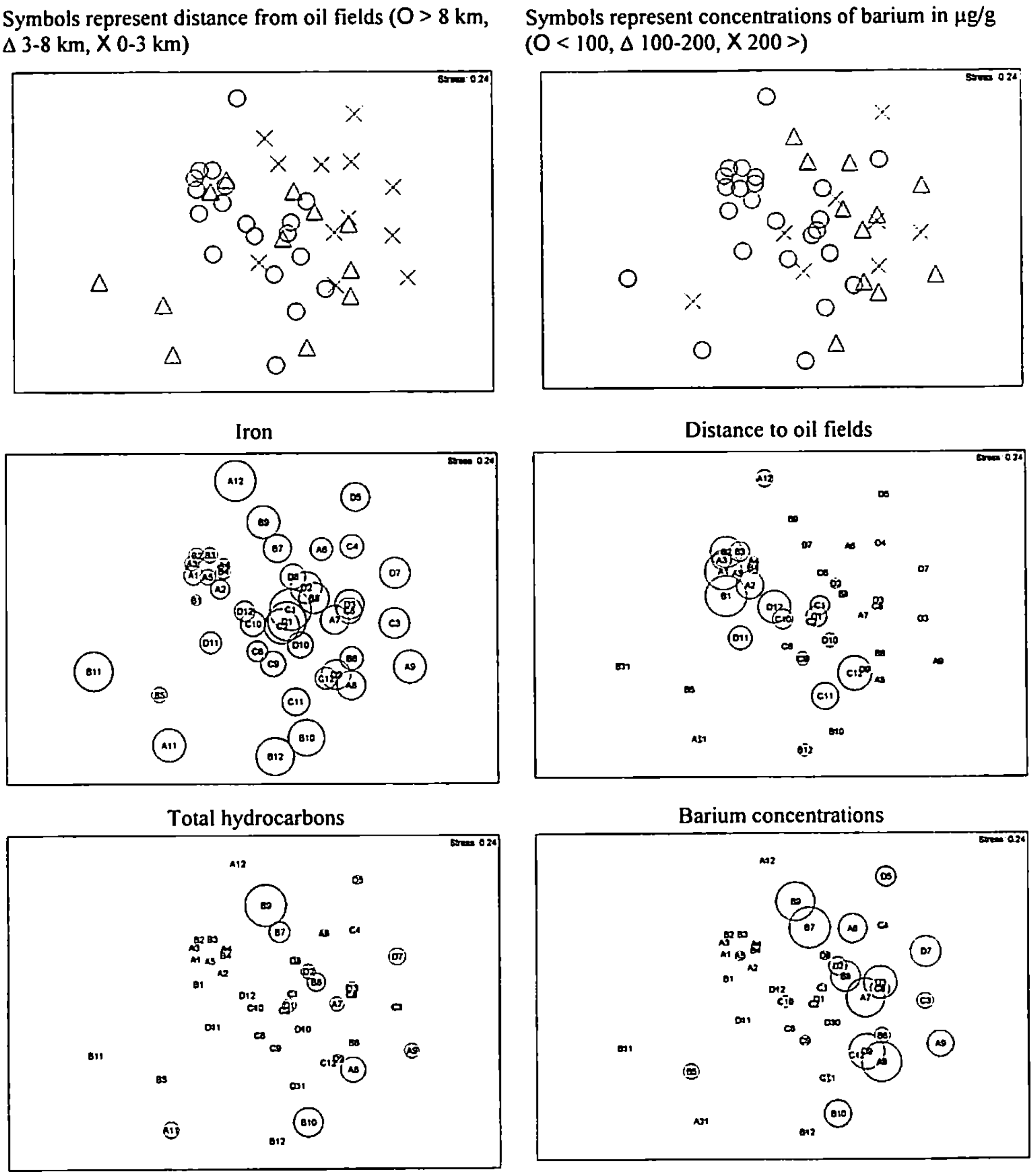


Figure 4.9. 2-d MDS ordination plots assemblage data for large macroinfauna during April 2000 based on Bray-Curtis similarities of abundance (fourth root transformed). Selected indicators of anthropogenic disturbance are superimposed on the abundance configuration. The size of the circle is directly proportional to the value of the variable.

Multivariate measures of community stress

Index of Multivariate Seriation (IMS): The results of the correlation of Bray-Curtis similarities of abundance data (fourth root transformed) calculated between every pair of samples within each season/fraction/transect combination against a linear sequence are given in Table 4.6. For small macroinfauna during November 1999 at the end of the rainy season, complete absence of seriation was detected on all four transects. During April 2000 after the 'northers' season, the correlation with a linear sequence was significant along transects A-B but not along C-D. For large macroinfauna, overall results along transect A-B were similar to that from the small macrofauna. However, along transect C, seriation was observed during both seasons, with relatively low values of the Index of Multivariate Seriation, although significant. In contrast, along transect D no seriation was detected during any season. To graphically represent this pattern of (or absence of) linear sequence, similarities along transects were re-ploted from the original Bray Curtis similarity matrix on fourth root transformed abundances (Figure 4.10). From the plot it can be noticed that the extreme ('controls') ends of the transects follow a line where consequently the middle stations would be expected to fit. However, major discontinuities can be observed, modified perhaps by natural disturbance from river runoff, but potentially affected by oil-related activities as these stations are located in the area of high oil fields density.

Index of multivariate dispersion (IMD): Table 4.7 presents the results of the relative dispersion within, and pairwise comparisons between, stations grouped by distance to oil fields or concentration of barium in the sediment. The relative variability within each group consistently showed that samples at 0-3 km and at 3-8 km distances were more dispersed than samples at >8 km away from the nearest platform. For the small macroinfauna during November, the highest IMD values occurred when comparing the 0-3 km group to the furthest and intermediate groups, i.e. similarities among samples in the furthest and intermediate groups are in general higher than similarities among samples closer to oil fields. However, during April, the 3-8 km and 0-3 km groups exhibited the smallest IMD value, suggesting similarities are more or less equal in both groups. Comparisons for the large macroinfauna were similar, but the largest IMD value occurred between the >8km group and the intermediate group. The relative dispersion and IMD values for the groups based on barium concentration showed no obvious pattern except for the small macroinfauna in November where the high concentration group was more dispersed than the other two.

Meta-analysis: The results of comparing the severity of disturbance from the Southern GoM to that encountered in the NE Atlantic using the meta-analysis training data are shown in Figure 4.11. On the left side of all plots are located the stations from the NE Atlantic where molluscs and echinoderms have relative high importance and on the right samples from the Southern GoM where crustaceans and sipunculids were more important. The pollution gradient of the NE Atlantic samples is along the vertical axis, going from unpolluted stations (U) at the bottom to gross polluted (GP) stations at the top of the plots. The distribution of samples from the Southern GoM along this axis varied with size of fauna and season. Stations presumably under gross pollution (i.e. GoM stations clustering with GP samples) only occurred during November. For the small macroinfauna, these were stations A9 and C4, and for the large macroinfauna A10 and B11; polychaetes had the highest relative contribution at all these sites. The vast majority of samples were located under the moderate pollution condition during November and unpolluted condition during April, but there was no clear pattern in relation to distance to oilfields or barium concentration (superimposition of symbols not shown). Impoverished sites where crustaceans, sipunculids or other phyla had a higher relative importance than polychaetes, were always located in the unpolluted section.

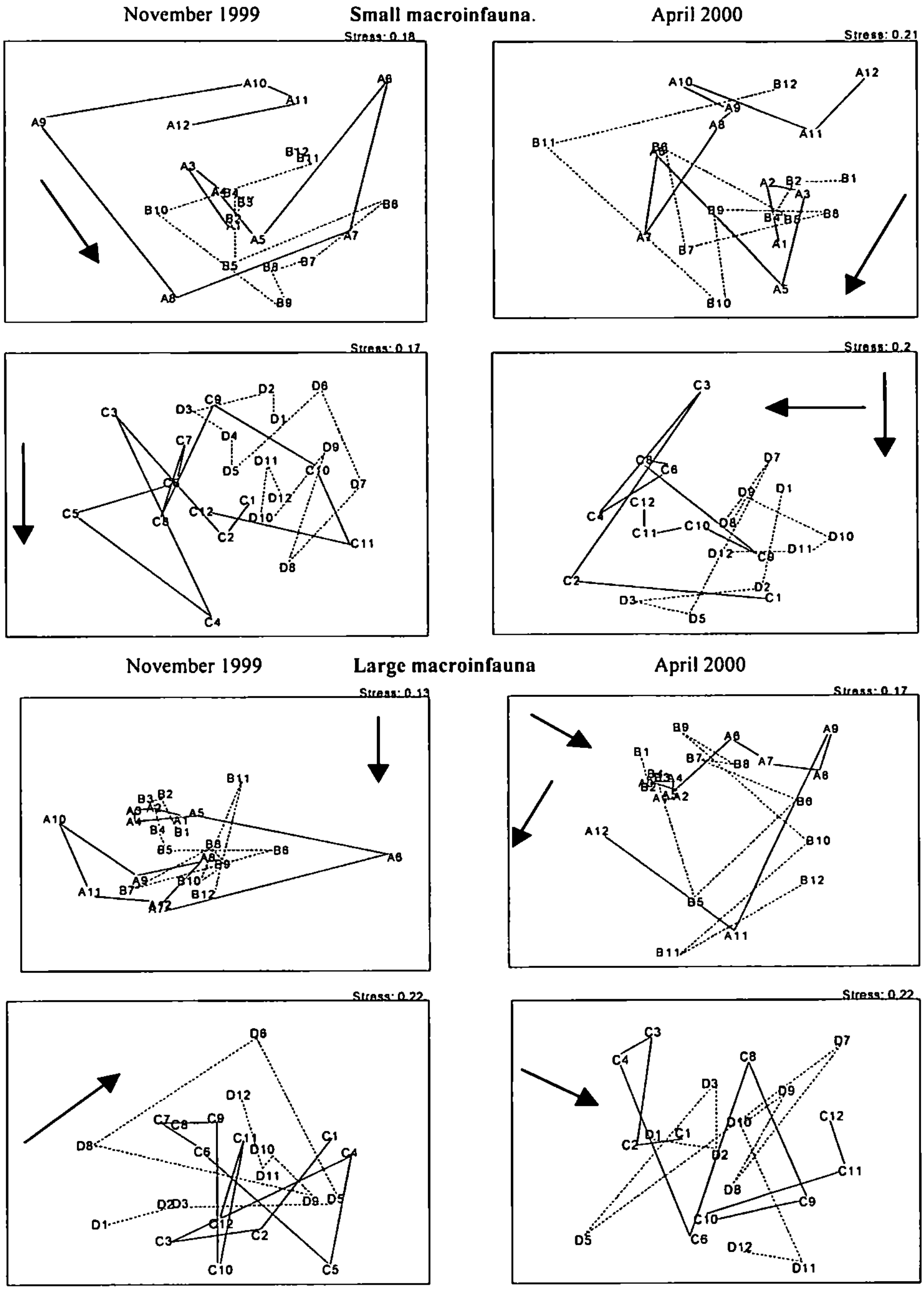
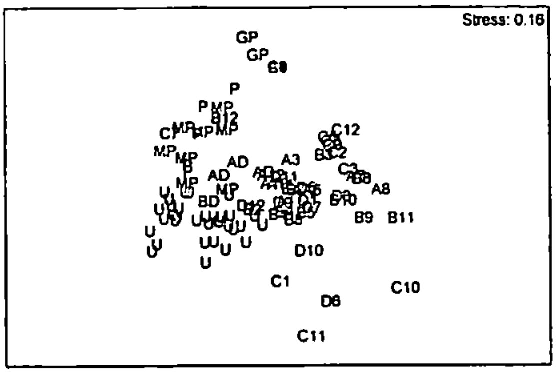
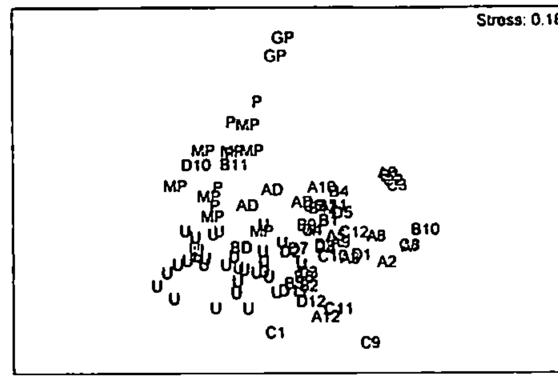


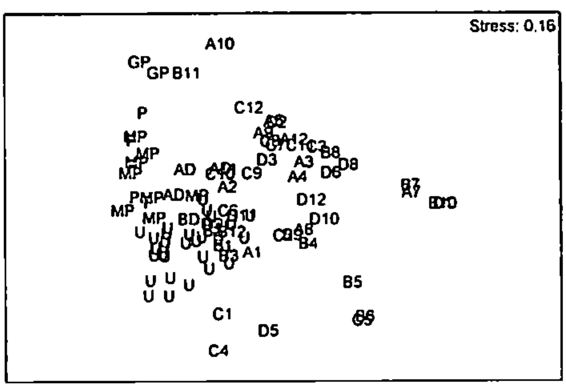
Figure 4.10. 2-d nMDS ordinations of the macroinfauna community (abundance data) along four transects (A-D) for two seasons and two size of macroinfauna. Arrows represent the linear assumption of change along each of the transects. Where the direction of change differs two arrows are displayed The lines indicate the degree of seriation from shallow to deep stations (A-B) and moving away from river influence along similar depth (C-D).



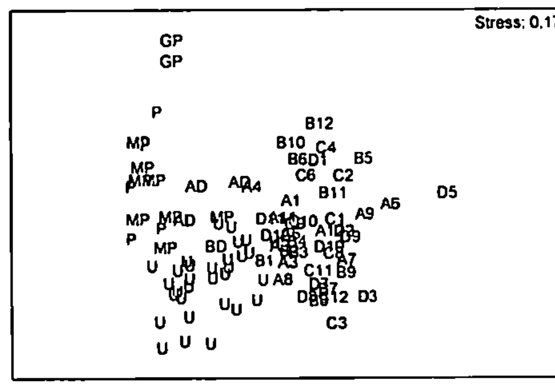
November small macrofauna



April small macrofauna



November large macrofauna



April large macrofauna

Figure 4.11. 2-d nMDS ordination plots of Meta-analysis of NE Atlantic (GP grossly polluted, P polluted, MP moderately polluted U unpolluted, BD biodisturbed, AD anoxic sites) and Southern GoM data along transects A-D for each fraction/season.

Table 4.6. Index of multivariate seriation (IMS) along transects A-D for each fraction/season. Figures in parenthesis are the % significance levels in a permutation test for absence of seriation in 999 simulations.

Small macroinfauna

Season	Transect A	Transect B	Transect C	Transect D
November 1999	0.062 (34.9%)	0.116 (20.2%)	-0.133 (83.4%)	0.207 (5.8%)
April 2000	**0.455** (0.3%)	**0.359** (1.1%)	0.17 (13.9%)	0.046 (39.2%)

Large macroinfauna

Season	Transect A	Transect B	Transect C	Transect D
November 1999	0.163 (12.3%)	0.211 (6.8%)	**0.355** (1.2%)	-0.017 (52.6%)
April 2000	**0.283** (2.2%)	**0.252** (4.9%)	**0.286** (4.8%)	0.052 (36%)

Table 4.7. Relative dispersion and Index of Multivariate Dispersion (IMD) between all possible pairs for small and large macrofauna sampled in November 1999 and April 2000. Groups based on a) distance to oilfields and b) barium concentrations

a) Dist to ilfields	November small macrofauna	November large macrofauna	April small macrofauna	April large macrofauna
>8km	0.789	0.878	0.901	0.869
3-8km	1.009	1.199	1.118	1.305
0-3km	1.306	1.042	1.111	1.035
Pairwise IMDS				
>8km, 3-8km	-0.229	-0.328	-0.212	-0.426
>8km, 0-3km	-0.51	-0.155	-0.215	-0.177
3-8km, 0-3km	-0.31	0.142	0.019	0.299
B) Barium conc.				
Low	0.711	0.941	1.012	1.002
Medium	0.948	1.132	0.969	1.056
High	1.14	1.02	0.96	0.959
Pairwise IMDS				
Low, medium	-0.255	-0.193	0.057	0.044
Low, high	-0.428	-0.079	0.035	-0.054
Medium, high	-0.2	0.111	0.03	-0.091

Discussion

For any impact study of oil-related activities, the contamination (i.e. increased levels of a chemical compared to natural background levels (GESAMP 1995)) status of the area needs to be proved in order to relate that contamination to changes in the fauna (Olsgard & Gray 1995). NAS (1985) reports that in unpolluted marine sediments Total Hydrocarbons (TH) seldom exceed 50 μg g^{-1} dry weight. Volkman *et al.* (1992) noted that organic rich sediments can have a TH concentration up to 100 μg g^{-1} dry weight, but concentrations above it are related to petroleum inputs. Generally in the Southern GoM the set threshold of TH for unpolluted sediments is 70 μg g^{-1} dry weight (Botello *et al.* 1991, Gold Bouchot *et al.* 1999). The present study reports a range of concentrations from not detected at the inner shelf to above 100 μg g^{-1} dry weight in the nearby of the oil fields. 90 to 100 % of the TH load was an Unresolved Complex Mixture (UCM) (see Appendix 4c) indicating a chronic input and highly weathered petroleum origin (NAS 1985, Volkman *et al.* 1992). Botello (1982) reported background levels of TH below 50 ppm and of biogenic origin in recent sediments of the transitional shelf. After the Ixtoc blowout in 1979, levels were above 100 ppm within the vicinity of the field (Boehm *et al.*, 1982), returning to background levels after 12 months (Botello and Villanueva, 1987). The development of the pattern of contamination by oil hydrocarbons has been followed by (Botello *et al.* 1991, Gonzalez *et al.* 1992, Jesus-Navarrete 1993), these authors highlighting that the distribution of petrogenic hydrocarbons is not restricted to areas adjacent to the oil fields. This study provides evidence that the distribution pattern of TH along transects clearly shows a signature of oil-related activities, with high concentrations at stations located within the oil activities zone and the influenced area extending beyond the designated oil activities area in the Southern GoM.

There is no published background information on concentrations of trace metals in the oil-exclusion zone and little is known about the amount of drilling fluids that have been discharged since oil exploration started in 1974. It is therefore impossible to know how high the present concentrations of metals and oil hydrocarbons are. Previous work has highlighted the increasing levels of metals towards the south and south-western portion of the Campeche Bank (Macias-Zamora *et al.* 1999). This is thought to be the result of river runoff and fine sedimentation. It also has been suggested that oil-related activities contribute to the concentration of barium, nickel, chromium and vanadium; (Rosales-Hoz *et al.* 1994, Rosales-Hoz *et al.* 1999). Levels of barium unequivocally indicate influence from drilling discharges (Kirkley 1984, Steinhauer *et al.* 1994, Rezende *et al.* 2002) and it has previously been showed that barium levels in the Southern GoM increased when approaching the oil activities zone (Rosales-Hoz *et al.* 1994). It appears that contamination from oil related activities extends beyond the immediate surroundings of the point source, as noted from the univariate plots of indicators of oil-related activities in this study. Additionally, results from the PCA ordination clearly show a change from the ordination pattern reported in Chapter 3 once hydrocarbons and metals were included. It is therefore concluded that the contaminated area in the Southern GoM is comparatively extensive and thus differs from the restriction of contamination to near the point source in the northern GoM (Middleditch 1981b, Kennicutt *et al.* 1996a). Extended contaminated areas and overlapping influences are expected from a long history of oil exploitation (Olsgard & Gray 1995) and that seems to be the case for the present area of study. Levels of hydrocarbons and metals were low across the inner shelf; but there is an absence of oil activities at depths <30m. Also, the current pattern from the northern shelf towards the SSW tends to transport selectively fine silt and clay particles offshore, thus preventing the transport of contaminated sediment from the oil activities zone towards the inner shelf.

Producing unequivocal evidence of pollution from offshore oil-related activities is a difficult task due to the pervasive effect of background variability linked to natural disturbance (Clark 1982, Spies 1987, Levin 1992). Temporal and spatial patterns of small and large macroinfauna in the Campeche Bank covaried with shelf-wide physical processes and followed the distribution of sediment type, depositional regime and intensity of natural disturbance (see Chapter 2). However at a smaller scale (transitional sedimentary environment) no clear gradients were observed moving away from the river influence, as noted from the distribution of biological variables along transects C-D (see discussion in Chapter 3). Most of the impoverished stations did not correspond to stations closest to the river influence, but to stations closer to areas of high oil rigs density or to a particular oilfield. Additionally, the absence of any depth-related zonation from 30-135 metres, and the increase in variability both in densities and community composition, contrast with the described patterns in other areas of the GoM (Flint & Holland 1980, Alexander *et al.* 1981, Phillips *et al.* 1990).

Severe contamination from oil-related activities can lead to azoic conditions, or at least severely reduced densities and number of taxa, resulting from smothering, organic enrichment and toxic effects at less than 500m from the point source. It also has been reported that within 500 to 1000m of a platform there is a reduction in diversity and an increased dominance of opportunistic species as several niches become vacant (Addy *et al.* 1984, Davies *et al.* 1984, Kingston 1987, Hyland *et al.* 1994, Daan & Mulder 1996b, Montagna & Harper 1996). In contrast to such severe effects, initial impacts can result in an increase in the abundance of some species and changes in the presence-absence patterns of rare species. These effects can be observed up to 2-3 km from the point source and, potentially, depending on the history of exploitation and local hydrology, up to 6km away (Gray *et al.* 1990, Kingston 1992, Olsgard & Gray 1995). Results from the ANOVA and ANOSIM clearly showed that stations located in areas of high oilrig densities, or closer to oil fields, had lower densities and biomass and generally an impoverished community composition; this effect was independent of season. These results do not, however, clearly identify the zonation described earlier since type of platform, history of production or types of discharge were not considered in the grouping.

Some aspects of the result of oil disturbance on the benthic infauna can be observed from the distribution of fauna along the transects, with extremely impoverished stations located in areas where oil rigs concentrate. The characteristic peak of opportunist taxa occurred at sites B8 and D7, with numerous copepods, ostracods, juvenile bivalves, and spionid and paraonid poychaetes present within the small macrofauna. However, several families of polychaetes (Capitellidae, Spionidae, Cirratulidae, Paraonidae, Lumbrineridae) that are know to contain opportunistic species had much higher abundances at sites where no oil activities are present i.e. the inner shelf. Thus the response of opportunists to natural and anthropogenic disturbance is not easily distinguishable.

The pattern of contamination seemed to explain substantially the patterns in biotic variables, (multiple regression analalysis and BIOENV procedure) supporting the evidence that pollution is occurring in the Southern GoM. However, the pollution effect is difficult to distinguish from natural disturbance along transects C-D since they received a stronger influence from river runoff, particularly immediately after the peak of the rainy season.

The previous chapter highlighted the absence of patterns of zonation of macroinfauna community structure at the scale of this study in the Southern GoM compared to the well-recognized patterns in other areas of the GoM and around the world (Rabalais & Boesch 1987, Sherman *et al.* 1988, Zijlstra 1988, Carey 1991, Coleman *et al.* 1997, Karakassis & Eleftheriou 1997, Gray 2000). Although the hypothesis of no differences among groups of stations either in areas of high oil rigs densities or close to oil fields was rejected, results from the multivariate ordination analyses did not clearly reflect the grouping of sites based on those criteria (except for the large macrofauna in April). Therefore, neither a clear zonation across shelf nor a clear pattern in relation to human disturbance was identified. However, the data were characterised by enormous variability, due for example to changes along depth gradients, the interaction of terrigenous and carbonaceous sediments (incorporating natural disturbance from river runoff) and winter storms supplementing the anthropogenic disturbance from oil related activities. The ability of multivariate techniques to detect effects of contamination is greater in areas where natural environmental variables and patterns of fauna distribution are homogenous (Olsgard & Gray 1995). Although sediment characteristics in the area of study are relatively homogenous if compared to the northern portion of the Campeche Bank, the range of disturbance from natural and oil-related sources is likely to account for much of the variability recorded for all biological variables (except H' diversity index).

The Index of Multivariate Dispersion indicated an increased variability for the group of stations located within 0-3 km to an oil field, or with high concentrations of barium in the sediment, indicating increased levels of stress (Warwick *et al.* 1990b, Warwick & Clarke 1993b). The scattering of sites within 3km from the nearest oil field resulted from the very low similarities in community composition, even between sites next to each other. This increased variability in the multivariate patterns can be explained by the documented response of infauna to both natural and oil-related disturbance. Natural disturbance related to river runoff is extensive, but it was expected to have a gradational influence that would decrease in effect away from the source. Natural disturbance might therefore produce an overall impoverishment in the area due to changes in deposition/erosion events when the river discharge peaks (see discussion in Chapter 3 and references therein). This period is followed by a recovery when opportunist species dramatically increase in numbers after a lag of several months, as observed at stations on the inner shelf. Although there is a natural patchiness in relation to the effect of the disturbance, the temporal response of impoverishment and peak of opportunists is driven mainly by the presence or absence of this disturbance.

In contrast, the offshore oil-related disturbance is usually represented by a progressive degradation of the benthic community structure, and the response of opportunistic species is known to represent the final stages of pollution resulting from continuous disturbance rather than being a recovery response to the absence of disturbance (Dicks & Hartley 1982, Gillmor *et al.* 1985, Spies 1987, Patin 1999). It is proposed that along transects C-D, and at the crossing of transects, impoverishment resulting from natural disturbance is aggravated at stations close to oil fields or in areas of high oil rig density. Here the recovery response, as observed on the inner shelf following the natural disturbance, is prevented by the continuous disturbance from oil-related activity. Therefore, when natural disturbance from the rainy season is absent, oil-related disturbance is clearly controlling the multivariate pattern of the large macroinfauna, as noted from the abundance ordination plot and superimpositon of levels of barium and distance to oilfields for the data from April. Pollution produces a recognised tendency to influence the size distribution of macroinfauna and meiofauna, with the opportunistic species being smaller for the former and larger for the latter, thus modifying the bimodal size distribution of meiofauna and macroinfauna (Warwick 1984, Warwick 1993, Warwick & Clarke 1996). The existence of this trend is demonstrated by large numbers of copepods and ostracods in the macroinfauna at sites B8 and D7, which are usually characteristic of meiofauna, and large numbers of particularly small spionids and paraonids at the lower end of the macrofaunal size range. The lack of differences between the <3km and 3-8km group, and the presence of depth as one of the best explanatory variables, indicates that natural variability is so strong that without proper controls (logistically impossible) or long-term observations, its contribution can not be separated from that of oil pollution.

The lack of appropriate controls and previous information on community structure on the area required the use of techniques that can overcome these problems and provide extra support to the general finding that impoverished sites are a result of oil-related activities. The ABC and Meta-Analysis method do not require spatial or temporal controls (Warwick 1986, Warwick & Clarke 1993a, Warwick & Clarke 1994). The ABC method showed that those stations located at the crossing of the transects, and at the south-western extreme of transects C-D, are polluted. This pollution pattern was not restricted to stations located in areas of high density of oilrigs or close to oil field, as some stations located on the inner shelf showed a disturbed condition. The ABC method was found to be useful in identifying natural and anthropogenic disturbance, mainly of organic origin (Warwick *et al.* 1987, Austen *et al.* 1989, Anderlini & Wear 1992, Warwick & Clarke 1994). However, this method can not determine what type of disturbance caused the actual pattern, neither has it been tested under toxic pollution (Roth & Wilson 1998). It can be inferred from this study that the disturbed configuration from stations on the inner shelf is more likely to be produced by natural disturbance from the heavy rainy season recorded in 1999, coupled with winter storms that influence the shallow parts of the shelf. Perhaps the most striking result of the ABC method was that several sites along transects C-D with a very impoverished community presented a non-polluted configuration.

The ABC method uses the changes in size distribution of macroinfauna that occurs under conditions of organic enrichment and/or physical disturbance. In general, this relates to changes in the numerical dominance of small opportunistic species, often present in large numbers, and the reduction in the contribution to biomass of large K-dominants that are more sensible to the disturbance (Warwick 1986, Warwick & Clarke 1994). Disturbance caused by oil-related activities is represented by organic pollution from the excessive load of oil hydrocarbons (and other compounds) in the drilling muds, but also by physical disturbance through smothering (Davies *et al.* 1984, NAS 1985, Kingston 1987). In both cases the observed opportunistic response is similar to that caused by organic enrichment and natural or anthropogenic physical disturbance (Oliver *et al.* 1980, Pearson 1987, Rees *et al.* 1992, Okey 1997, Newell *et al.* 1998, Kaiser 2000, Chivilev & Ivanov 1997). Additionally, oil-related disturbance involves a toxic stress from trace metals and PAHs contained in the drilling muds, and as a result of any accidental spills (Anderson *et al.* 1974, Menzie 1982, Lee & Page 1997, Grant & Briggs 2002, Holdway 2002). The response of the benthic macroinfauna community to such toxic stress is a reduction in both number of species and densities, also preventing the classic response of opportunistic species through direct mortality or a reduced settlement of new recruits (Gray 1979, 1982, Addy *et al.* 1984, Olsgard & Gray 1995). Under toxic stress perhaps the ABC method is not able to discern a disturbed pattern, as changes in the proportion of abundance and biomass dominants are not produced by increases in numbers of opportunists.

The Meta-Analysis results were inconsistent in terms of defining the status of sites close to the oilfields in respect to a known pollution gradient. A general observation from the results is a clear split of the samples from the NE Atlantic from those of the Southern GOM; this split has been previously reported from data off Trinidad and Tobago (Agard *et al.* 1993). These authors proposed that the split could be due to the estuarine character of their study site, but this explanation is not convincing for the GoM data. It is proposed instead that the split maybe due to latitudinal differences, driven by the greater proportional contribution of phyla that are not so numerous in the NE Atlantic (e.g. sipunculids). Another aspect of the method is that the polluted status is based on the major contribution of polychaetes as they contain a great number of opportunistic species known to dwell in areas with organic enrichment (Warwick & Clarke 1993a, Warwick & Clarke 1994). However in the Campeche Bay, several impoverished sites where polychaetes contribute little were clustered with the unpolluted sites. The method does not differentiate between natural and anthropogenic disturbance either, as most of the samples from November were classified under the moderately polluted condition, which may be more related to stress imposed by the rainy season. The fact that the area of study is naturally disturbed makes both the ABC and meta-analysis methods inconclusive in terms of determining what is producing the disturbed configuration and again natural disturbance is confounding the pattern from oil-related disturbance.

Finally, two fairly new multivariate techniques were used to assess the disturbed condition of the sampling area in general, the Index of Multivariate Dispersion (IMD)

(Warwick & Clarke 1993b) and the Index of Multivariate Seriation (IMS) (Clarke *et al.* 1993). Both techniques are based on the assumption that stress from disturbance, or pollution, increases the variability in community composition, and although this increase in variability is a recognised feature it has been little explored. The IMDS was discussed previously, so the following section will focus on the results of the IMS. The technique detailed in (Clarke *et al.* 1993) aims to identify changes along a linear sequence of samples on a transect where neighbouring samples are more similar than distant ones consistent with a theoretical linear sequence. Zonation across shelves may be summarised as a linear sequence of changes in community composition along depth gradients. For example, sites from shallow portions of the shelf (less than 30 m depth in the present study) tend to be more similar in terms of community composition than between samples from the middle (30 to 50 m depth) or outer shelf (>50m depth). This model of zonation would produce a multivariate ordination with defined clusters of samples corresponding to different sections of the shelf. Where benthic communities would be structured by across-shelf changes in food supply, light penetration, patterns of sediment re-suspension and transport and patterns of disturbance that change with depth of the water column. Thus, some degree of seriation would be expected to occur across the continental shelf of the Southern GoM. The IMS results showed some degree of seriation along the depth gradient during April but no seriation at all during November. If the assumption of expected seriation across the shelf is a valid one, then the breakdown of this seriation during November could be related to the interaction of natural and anthropogenic disturbances across the middle shelf. Moreover, the observed pattern of samples on the ordination plots indicate that stations in the middle of the transects (i.e. close to oil fields or in areas of high oilrigs density) are responsible for the low correlation values of the IMS and thus the consequent breakdown of seriation.

The present sampling design attempted to take into account the main sources of natural disturbance in the area by sampling macroinfauna after the rainy and winter storms season; macroinfauna is known to present an integrated response over time. It also tried to capture the putative oil-related influence by sampling over a range of sedimentary conditions and distances to oilfields. From all the results it was clear that control sites are not available in this region because of the background natural disturbance and the long-term presence of oil hydrocarbons from natural seeps. Despite the lack of adequate controls with which to contrast the results, it is considered that there is enough evidence to conclude that oil-related activities in the Southern GoM are having an impact on the macroinfauna community. This conclusion is based on the coincidence of the most impoverished stations with the areas of high density of oilrigs. Additionally, there was a reduction, or even an absence, of temporal changes in densities and number of taxa of these sites when compared with the inner-shelf stations that clearly responded to the seasonal decrease in river influence. Finally, evidence from impact comes from the patchy community composition that reflects a very simple structure at some stations, and a high overall variability in community composition at stations located within the oil activities zone. Although it is considered that the above evidence supports the existence of impact from oil-related activities, no definitive conclusions can be drawn regarding the magnitude of the influence of oil-related activities, since natural disturbance is also contributing to the variability in the area.

CHAPTER 5

CONCEPTUAL MODEL AND AN OVERVIEW OF VARIABLES CONTROLLING MACROINFAUNA COMMUNITY STRUCTURE OF THE SOUTHERN GULF OF MEXICO

Introduction

Similar to other continental shelves, those of the GoM are highly productive, constitute sinks for organic carbon and are under increasing pressure from coastal habitat alteration, increasing fishing effort and intensive oil related activities (Botello *et al.* 1982, Walsh 1988, Sherman 1994, Patillo & Nelson 2000, Vazquez *et al.* 2000). The functioning of the continental shelves in the Southern GoM is tightly coupled to the influx of oceanic water from the Caribbean, coastal interactions through river runoff and atmospheric interactions via northern cold fronts (Biggs 1992, Carranza-Edwards *et al.* 1993, Escobar-Briones & Soto 1997, Fuentes-Yaco *et al.* 2001). Water column productivity and pelagic biota are influenced by changes in direction and strength of the northern intrusion of the loop current, intensity of river runoff, interactions of freshwater and oceanic fronts and seasonal mixing by winter storms (Yañez-Arancibia & Sanchez-Gil 1983, Ruiz Renteria & Merino Ibarra 1989, Licea & Luna 1999, Walker *et al.* 1999, Sanvicente-Añorve *et al.* 2000). Less is known of the effect of these influences on benthic communities, although information available indicates that carbon from terrigenous sources is consumed by benthic infauna (Soto & Escobar-Briones 1995, Soto *et al.* 1998).

Rabalais *et al.* (1999) in their overview of the benthic communities of the GoM described the driving factors that affect benthic communities at the scale of the whole Gulf. Although similar factors (e.g. sedimentary regime, depth and depth related processes, temperature, riverine flux and extreme events such as tropical storms) are thought to structure benthic communities in the Southern GoM, there is still a lack of quantitative data on the magnitude of their influence. Throughout chapters 2-4 an attempt has been made to quantify the influence that the aforementioned large-scale process have on the benthos and the interaction with the putative influence from oil related activities. It is the aim of this chapter to integrate the results previously described and construct conceptual models that describe, in general, the benthic macroinfauna community structure and its driving mechanisms in the context of existing models for sub-tidal benthic communities under natural and anthropogenic disturbance.

Mechanisms that control benthic community structure

From the numerous attempts at classifying marine benthic communities, the role of environmental variables stands out in structuring macroinfauna (Jones 1950, Thorson 1955, Mills 1969). The mechanisms by which environmental factors structure marine benthic communities are scale dependent (Andrew & Mapstone 1987, Beukema *et al.* 1996, Thrush *et al.* 1999), such as the classification of sub-tidal benthic communities from the North Sea (Glemarec 1973) where thermal stability of the water column is proposed to be the main driving variable at the scale of the whole North Sea. However, smaller scale variability within Glemarec's 'coastal etages' are produced by differences in sediment structure, content of organic matter, hydrology regime and depth (Eleftheriou & Basford 1989, Barry & Dayton 1991, Basford *et al.* 1996). Animal-sediment interactions play an important role at small scales where variability in sediment structure and composition, macroinfauna feeding types, larval settlement and the local hydrology regime structure benthic communities in a patchy way (Gray 1974, Rhoads 1974, Butman 1987, Reise 1991).

Models that describe the mechanisms controlling benthic community structure and sediment-animal interactions have been succinctly summarised by Zajac and Withlach (1985) and Zajac *et al.* (1998). They pointed out that environmental, life history and biotic interactions are the most common approaches used, each providing different views of the successional dynamics of benthic communities and are hierarchically inter-linked. Existing models focus mainly on one or two of the hierarchy levels. For example, the Trophic Group Amensalim Hypothesis (TGAH) regards sedimentary environments and biotic interactions as the controlling variables (Rhoads & Young 1970), although it has a limited scope as pointed out by Hall (1994). The Trophic Group Mutual Exclusion (TGME) model states that benthic macroinfauna composition, biomass and productivity are food limited and water flow constitutes the exclusion factor controlling food and inhibiting particular trophic associations (Wildish 1977, Wildish & Kristmanson 1997). Whilst the organic enrichment model of community structure and succession suggest food availability is the most fundamental variable underlying the structure of marine benthic communities, modified by depth and water flow (Pearson & Rosenberg 1978, 1987, Pearson 2001).

The discussion as to wether sediment *per se*, or the physical regime coupled with biotic interactions, ultimately drive community patterns on sedimentary environments (Jones 1950, Gray 1974, Rhoads 1974, McLusky & McIntyre 1988, Lenihan & Micheli 2001) appears to be moving towards models of multiple interactive variables, where the benthic boundary layer flow is receiving increasing attention (Nowell & Jumars 1984, Snelgrove & Butman 1994, Wildish & Kristmanson 1997, Whitlatch *et al.* 1998). It is within the hierarchical inter-linked approach of environmental, life history and biotic interactions that community patterns in the Southern GoM will be interpreted in the following sections.

General patterns of benthic macroinfauna community structure on the Campeche Shelf

At a scale of >100 km, community composition of benthic macroinfauna on the Campeche Shelf was characterised as distinct assemblages within the carbonate and transitional sedimentary provinces. The carbonate assemblage was numerous and diverse, influenced by a heterogeneous sandy to sandy mud substratum (with numerous shallows, banks and reefs) with low organic matter, high carbonate content and high transparency of the water column. in comparison, the muddy transitional shelf had an impoverished community on a relatively homogenous soft bottom substratum, with a large mud patch on the middle shelf, and probably turbid bottom water with high organic matter content and a high amount of terrigenous mud (Chapter 2). Despite the lack of substrate heterogeneity, the transitional shelf showed great variability in community composition at the scale of tens of kilometres, and no discrete association of sites in relation to sediment type or water depth, except for the marked change on the inner shelf (Chapter 3).

At the scale of the whole Campeche shelf, the distribution of macroinvertebrates fits the general pattern of macrobenthos community structure across continental shelves, with a decreasing gradient of densities and biomass from the inner shelf towards the shelf break (McLusky & McIntyre 1988, Sherman *et al.* 1988, Zijlstra 1988). This across-shelf gradient is coincident with changes in shelf topography (e.g. changes in slope), patterns of general hydrology, water column stability and depositional patterns that influence food supply through advection and sedimentation from the water column (Glemarec 1973, Flint 1981, Eleftheriou & Basford 1989, Basford *et al.* 1996, Albertelli *et al.* 1999).

Temporal differences on the Campeche Shelf are driven by natural disturbances from 'northers' (or winter storms) and riverine deposition acting at different times and spatial scales. Severity of 'northers' (measured as amount of impact on macroinfauna densities) is greater on the carbonate shelf, as sandy sediments tend to be more loose and easier to re-suspend. Mortality probably results from abrasion and passive transport, thus explaining the low values of biological variables on the carbonate shelf following the 'northers' season (Chapter 2). The influence of river runoff increases the load of fine sedimentation and bulk organic matter onto the south-western area of the Campeche Shelf. The muddy environment, due to its cohesive properties, damps the wave and current effect minimising wave disturbance. This reduces the effect of winter storms, although this consequently leads to an increase in water content and sediment instability (Berlamont *et al.* 1993, Teisson *et al.* 1993). Immediately after the rainy season, values of biological measures were low, but the severity of disturbance was contingent with depth (Chapter 3).

Table 5.1 compares densities and biomass of macroinfauna observed in the Southern GoM to other studies within the GoM and on other continental shelves around the world. Although direct comparisons are not possible because of differences in sample and sieve size used, in general, where disturbance is present, densities tend to be low regardless of sediment type, particularly in areas where the disturbance is produce by river deposition. Few of these listed studies have observations of biomass and the measuring method varies widely, but it can be noticed that biomass in the Southern GoM is low compared to temperate regions such as the North Sea or Georges Bank.

Response of soft bottom macroinfauna to natural disturbance

On the Campeche Shelf, changes in the hydrology regime, increasing wave-disturbance caused by 'northers', and fine sedimentation from river runoff together with water column instability are crucial components of the ecosystem structure and function (Yañez-Arancibia & Sanchez-Gil 1983, Soto *et al.* 1998, Escobar-Briones *et al.* 1999, Fuentes-

Yaco *et al.* 2001). The documented response of infauna to natural disturbance from periodic storms and seasonal sedimentation through river runoff includes total defaunation (Rhoads *et al.* 1985, Aller & Todorov 1997, Armonies *et al.* 2001), physical and physiological stress with subsequent mortality (Moverley *et al.* 1986, Peterson & Black 1988, Nordby & Zedler 1991) and displacement by erosional and depositional events (Oliver *et al.* 1980, Thistle *et al.* 1991, Okey 1997). Following such disturbances, changes can occur in the intensity of biotic interactions and bioturbating activities (Brey 1991, Wilson 1991). In Chapters 2 and 3, the response of macrobenthos to natural disturbance was analysed in detail and it was noted that at the scale of the whole Campeche shelf, temporal variability is significant. The coincidence of the minimum values of densities and number of taxa just after the 'northers' season (Figure 5.1) suggests a link between mortality of macroinfauna and wave action related to increasing wind stress.

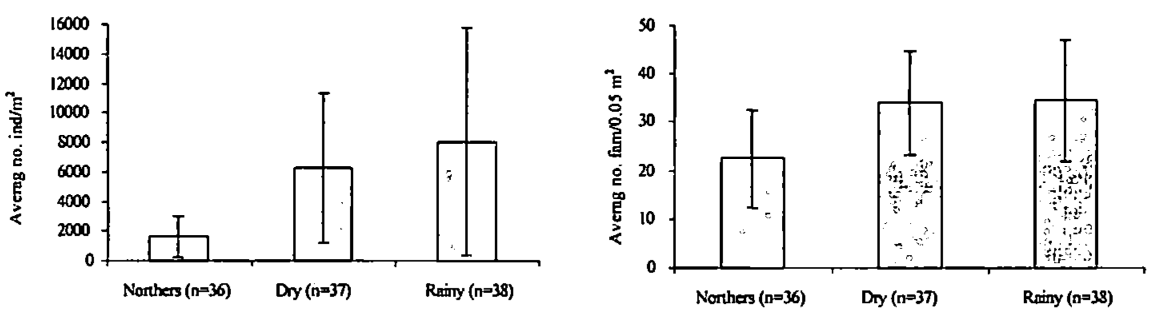


Figure 5.1. Average densities and number of families per replicate during each of the three main seasons in the southern GoM (sampled in 1993 using a 1.0 mm sieve). Error bars represent one standard deviation from the mean (see chapter two for detailed explanation of patterns).

The transitional shelf is subjected to fine sedimentation and water column instability caused by river runoff during the peak of the rainy season (July to September/October) followed by an increase in wave disturbance during the 'northers' season. Thus, an increase in severity of disturbance can be identified from the carbonate to the transitional shelf due to the combined influence of river runoff and winter storms, preventing the establishment of any community as rich and numerous as that from the carbonate region (Figure 5.2). Increasing the severity of disturbance increased overall variability, and thus resulting in smaller between season differences. This is due not only to natural factors but also, probably, from the anthropogenic stress of oil activities and naturally occurring oil seeps.

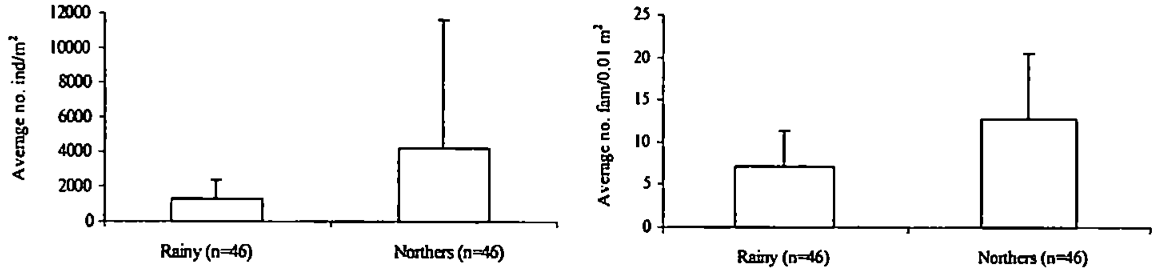


Figure 5.2. Average densities and number of families per station after the rainy and 'northers' season in the transitional shelf (sampled in 1999-2000 using a 0.5 mm sieve). Error bars represent one standard deviation from the mean (see chapter three for detailed explanation of patterns).

Figure 5.3 illustrates the spatio-temporal patterns of the disturbance regime in the SGoM. 'Northers' influence a larger area and putatively produce a disturbance of greater magnitude contingent with the sedimentary environment and depth. Typically there have been 15 to 27 northers every season from 1980-1998, and a relatively high number (26) occurred during the winter of 92-93 (Magaña *et al.* 2001). River runoff from the Grijalva-Usumacinta system probably has two peaks of flow linked to the rainy season (Magaña *et al.* 2001) and influences a smaller spatial area. The rainy season of 1999 was particularly heavy and its influence might be accentuated by bottom current patterns that transport fine sediments in a N-NE direction on the Campeche Shelf (Rosales-Hoz *et al.* 1999). A third disturbance from oil-related activities is represented as having a much smaller scale of influence, although its intensity is assumed to remain constant throughout the year. It has been present for 3 decades in addition to the naturally occurring oil seeps. Clearly, disturbance would be more intense in areas where river runoff and 'northers' occur sequentially and even greater where oil-related activities exist, the three factors having a cumulative influence.

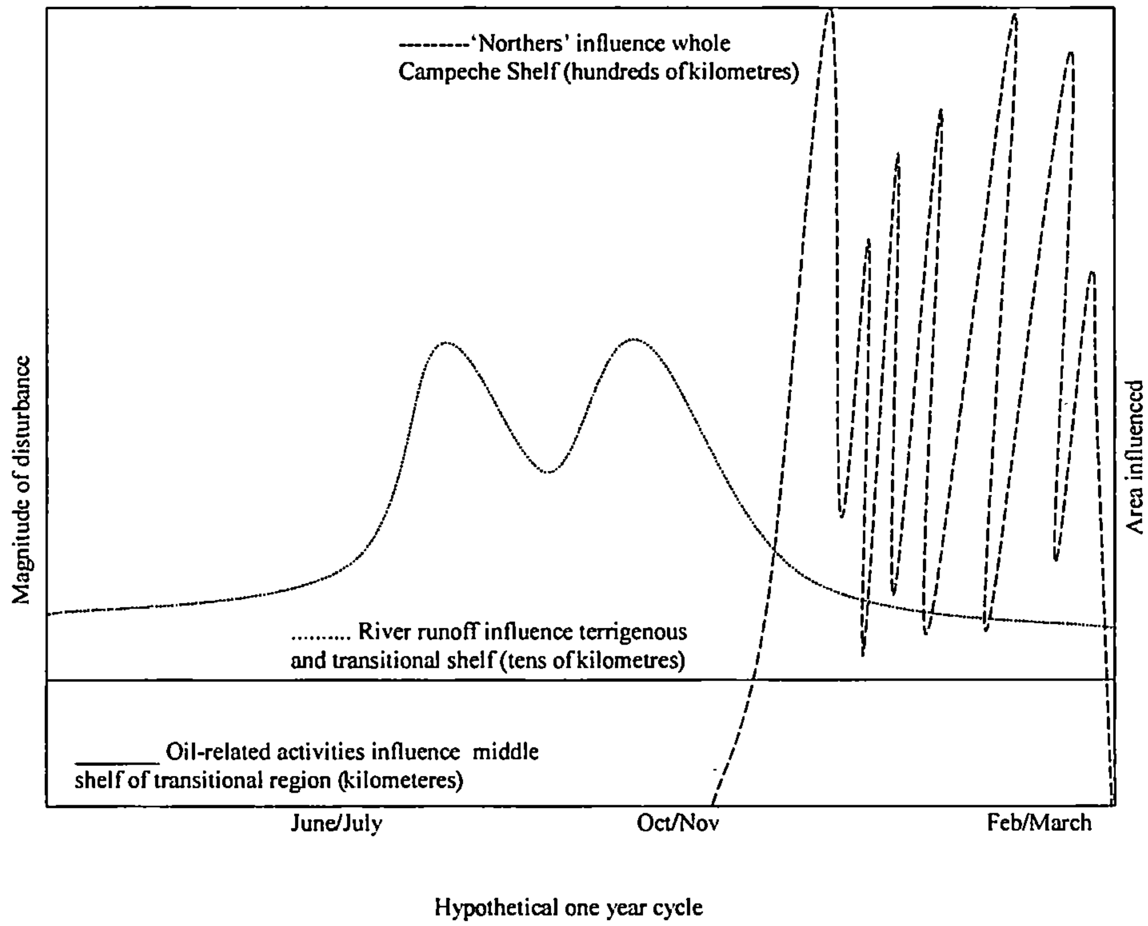


Figure 5.3. Conceptual model of the natural disturbance regime in the SGoM showing the extent of influence of 'northers', river runoff and oil related activities. The magnitude of disturbance is assumed to be contingent with the sedimentary environment and yearly variation.

Typically, after a disturbance event there is a recovery period where opportunist species increase in numbers (Aller & Aller 1986, Posey *et al.* 1996, Okey 1997). This recovery in the SGoM appears to have a lag of up to 4 months; however, the extent of the recovery period is restricted by the natural disturbance regime. The general response on the carbonate shelf is described conceptually in Figure 5.4a where a 'single' disturbance, e.g. 'northers', allows for a long period of recovery that reaches a peak of densities and number of taxa probably just before the following set of storms. Conversely, on the transitional shelf the recovery period is shorter due to a sequence of disturbances from river runoff and winter storms (Figure 5.4b). Additionally, there are probably two peaks of biological response resulting from the input of organic material as food for the benthic community (Soto & Escobar-Briones 1995, Soto *et al.* 1998). Although the data presented in Chapters 2 and 3 support this general model, the observed response does not necessarily follow a yearly cycle because it might be coincident with extreme conditions of 'northers' and river runoff as was the case for the 92-93 winter period and the 99 rainy season.

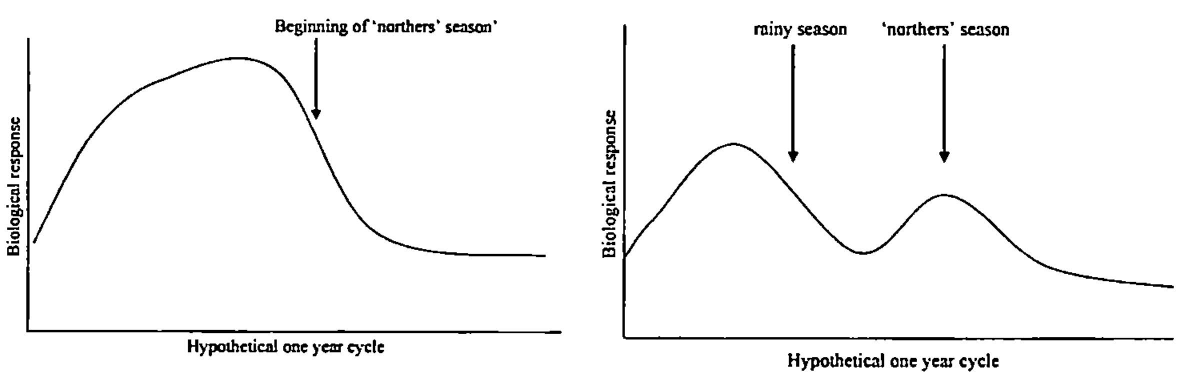


Figure 5.4. Generalised response of the macrobenthic community to natural disturbance within the SGoM over a hypothetical yearly cycle. a) Describes the biological response to a 'single' disturbance ('northers') on the carbonate shelf and b) the response to a sequence of disturbances (river runoff and 'northers') on the transitional shelf.

Response of soft bottom macroinfauna to anthropogenic disturbance in the southern Gulf of Mexico

The generalised model of response of benthic communities to organic enrichment (Pearson & Rosenberg 1978) is perhaps the most widely used to explain changes in benthic community structure along gradients of anthropogenic disturbance. At the extreme of maximum disturbance, (e.g. organic enrichment (Millner 1980, Pearson 1980); physical disturbance by dredging and fishing (Kaiser 1998, Newell *et al.* 1998); smothering by dumping (Messieh *et al.* 1991), sewage sludge (Rees *et al.* 1992, MAFF 1993), oil spills and drilling fluids (Suchanek 1993, Lee & Page 1997, Holdway 2002)) total defaunation can result, or at least cause a severe reduction in densities, biomass and number of species.

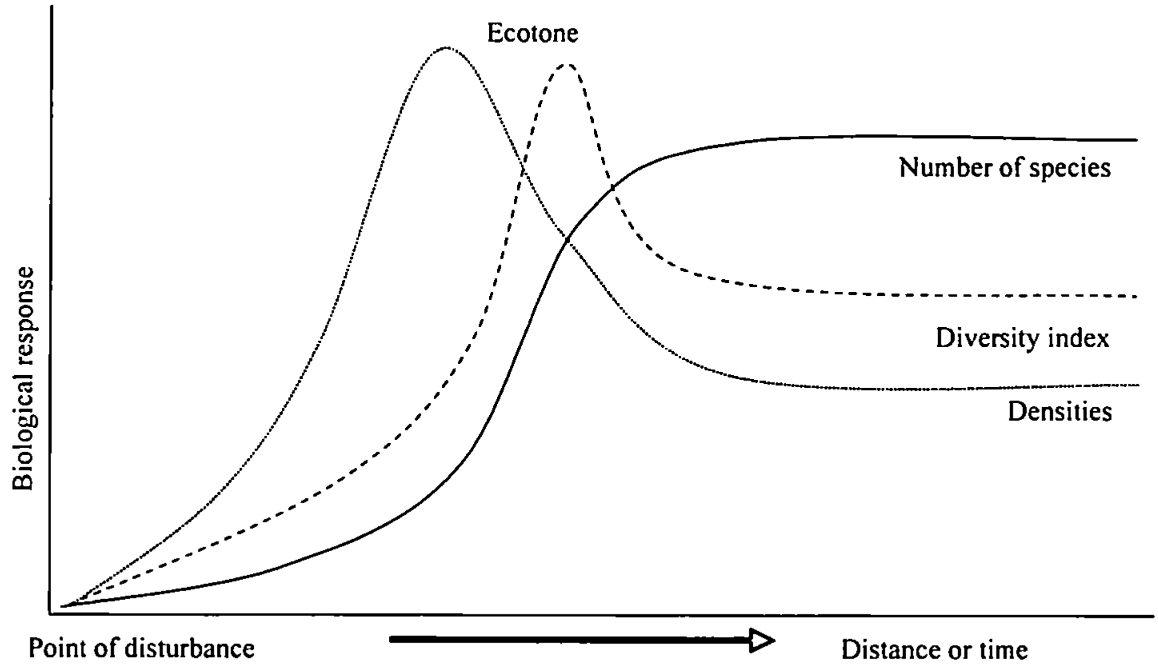


Figure 5.5. General biological response of macrobenthos to anthropogenic disturbance from a point source based on Pearson and Rosenberg's (1978) general model of organic enrichment.

Moving away from the source of disturbance, there is an increase in densities of opportunistic species whose reproductive and dispersive strategies allow them to colonise and exploit space and available food. At some point along the gradient a peak in diversity (i.e. the combination of number of species and evenness) occurs which represents the ecotone between undisturbed and moderately disturbed communities (Figure 5.5).

In offshore areas disturbed by oil activities, the benthic community response follows the above general model of response to organic enrichment. The most severe disturbance occurs within the immediate surroundings of the oilrig (Addy *et al.* 1984, Davies *et al.* 1984, Neff *et al.* 1989, Daan *et al.* 1990, Montagna & Harper 1996), produced by the combined effect of smothering (Hyland *et al.* 1994) and toxicity (Neff 1987, Carr *et al.* 1996, Grant & Briggs 2002). Further away is the peak of opportunist species, attributed to organic enrichment, and finally the return to background levels of community composition (Addy *et al.* 1984, Kingston 1992, Daan & Mulder 1996b). This general response occurs following a gradient from a point source of disturbance (Figure 5.5), but may not emerge in areas where combined disturbances control community structure (Harper *et al.* 1981b, Sharp & Appan 1982), as is the case in the offshore oil activities zone of the transitional shelf from the Southern GoM. This area is a depositional one known to contain high amounts of organic matter (see Chapter 3 and Cruz-Orozco *et al.* (1994)), and the general model of organic enrichment would predict high densities of opportunistic species. However, the influence of river runoff, physical disturbance from smothering (erosional/depositional events) during peak discharges, additional re-suspension and transport during the 'northers', plus probably low quality of food, causes a naturally impoverished area for macroinfauna. The influence of offshore oil-related activity produces additional smothering and organic enrichment and this organic load promotes populations of oil degrading bacteria (Lizarraga-Partida *et al.* 1991, Ford 2000). Figure 5.6 illustrates the biological response of the macrobenthos from the oil-exclusion area in the SGoM. The macrobenthic community is naturally impoverished as a result of river runoff and winter storm disturbance (broken line on Figure 5.6a, but also see Figure 5.4b). Moreover, the combined effects of natural and anthropogenic disturbance cause extremely low values of biological measures (see Chapter 4) reducing seasonal differences as a result of increasing variability (Figure 5.6b). The overall pattern then will present a small period when the disturbance is at its lowest (i.e. in the absence of peak river runoff and winter storms). It will be the only time when opportunistic species can recover.

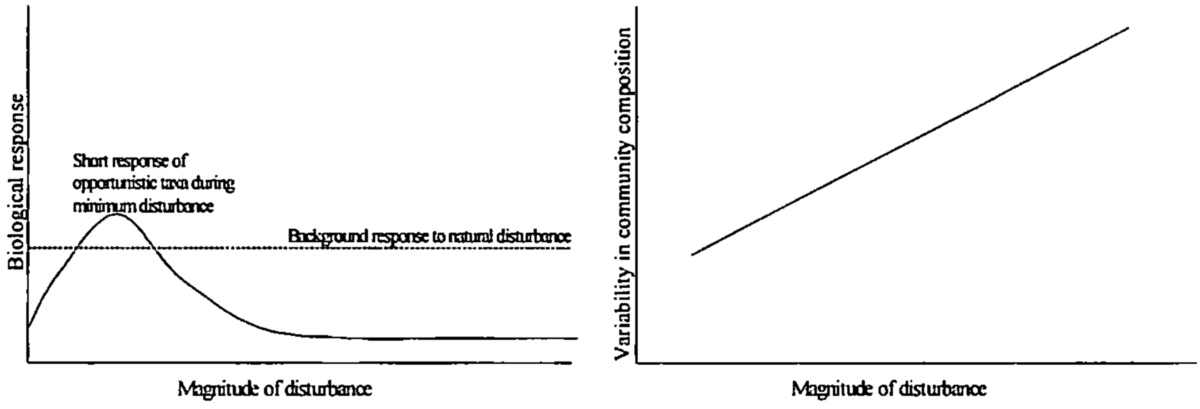


Figure 5.6. General response of the macroinfauna community from the transitional shelf of the Southern GoM to the combined influence of natural and oil related disturbance. a) Extremely low values of biological measures result from additional anthropogenic disturbance compared to the response to background natural disturbance. b) Increased variability in community composition as a result of increasing levels of disturbance.

Oil-related activity has an additional toxic effect difficult to evaluate in field surveys, and it can only be guessed at based on correlation with levels of metals and hydrocarbons. It has been suggested that the effects of organic enrichment and toxicity are opposed. The former causes an increase in numbers of opportunistic species and the latter a decrease in numbers of sensitive species, mainly affecting rare species and leading to local extinction (Gray *et al.* 1990, Kingston 1992, Olsgard & Gray 1995). This increase in local extinction of rare species as a result of toxicity effects will lead to an increase in variability of community composition (Pearson & Mannvik 1998). The influence of oil disturbance on the benthic community of the Campeche Shelf stands out from that of natural disturbance by inducing greater variability in community composition. This increase in variability reflects the patchy nature of the oil-related influence and the sequential effect of natural disturbance (Figure 5.6b). Local extinction around platforms as a result of combined effects of natural and anthropogenic disturbances, potentially allow for the vacant niches to be colonised through dispersal from neighbouring areas. However, if those neighbouring areas are also under periodic natural disturbance then supply of colonisers is probably restricted, a situation that would worsen the general impoverished condition and increase levels of variability in macroinfauna of the middle transitional shelf in the Southern GoM.

Direct comparison with existing models of benthic community response to offshore oil activities is not possible since this study did not follow a point source approach but rather a regional one. Nonetheless, there are similarities in relation to the spatially patchy response of the benthic community, as well as the increase in variability in community composition. The benthic community response is site specific and will depend on the type of effect experienced, i.e. smothering, organic enrichment or toxicity (Kingston 1987). The response has a patchy distribution related to the prevailing hydrological regime, history of exploitation and type of drilling fluid discharged (Trefry *et al.* 1985, Bakke *et al.* 1989, Daan & Mulder 1994, Olsgard & Gray 1995, Grant & Briggs 2002). The high variability in community composition at the family level suggests that the strength of disturbance is high and any adaptive response of the individuals, species and genus has been overcome and changes can be detected at higher taxonomic levels (Pearson & Rosenberg 1978, Warwick

1988a, Ferraro & Cole 1990, Warwick & Clarke 1993b). This is also consistent with Gray's (Gray 1979, 1982) observations on local extinction that undoubtedly lead to an increase in variability and underlies the assumption that higher taxonomic levels are more suitable for identifying anthropogenic impact (Warwick 1988b, Ferraro & Cole 1992, Warwick & Clarke 1993a, Warwick & Clarke 1994).

Hierarchical conceptual model of the benthic macroinfauna community structure on the Campeche Shelf

Environmental gradients constitute the highest hierarchical level of control over community structure since they do not only influence large physical areas but also the whole range of biological hierarchies (Zajac *et al.* 1998). The controlling influence of hydrodynamics on both sediment structure and food supply is considered to be the main mechanism structuring benthic communities on continental shelf areas around the world (Hyland *et al.* 1991, Schaff *et al.* 1992, Grebmeier 1993, Rossenberg 1995, Kube *et al.* 1996, Danovaro & Fabiano 1997, Albertelli *et al.* 1999). However, the influence of food supply on benthic macroinfauna is dependent on food quality rather than quantity (Karakassis & Eleftheriou 1997, Dauwe *et al.* 1998).

On the Campeche Shelf, at a regional scale the gradational response of macrobenthic community structure is determined by the environmental gradients represented in Figure 5.7. The transitional province of the Campeche Shelf is characterised by turbid bottom waters (Yañez-Arancibia & Sanchez-Gil 1983), water column instability (Monreal-Gomez *et al.* 1992), deposition of fine terrigenous material with high content of refractory bulk organic matter (Hedges & Parker 1976), input of pollutants from oil related activities

(Botello *et al.* 1996) and seasonal changes in the water current pattern (Boicourt *et al.* 1998, Martinez-Lopez & Pares-Sierra 1998, Rosales-Hoz *et al.* 1999). In contrast, the carbonate shelf is characterised by high water transparency and, perhaps, frequent upwelling on the northern Yucatan Peninsula (Ruiz Renteria & Merino Ibarra 1989, Walker *et al.* 1999) that supplies a higher food quality for the benthic community through benthic primary production and advective processes driven by the unidirectional flow of a branch of the Yucatan current.

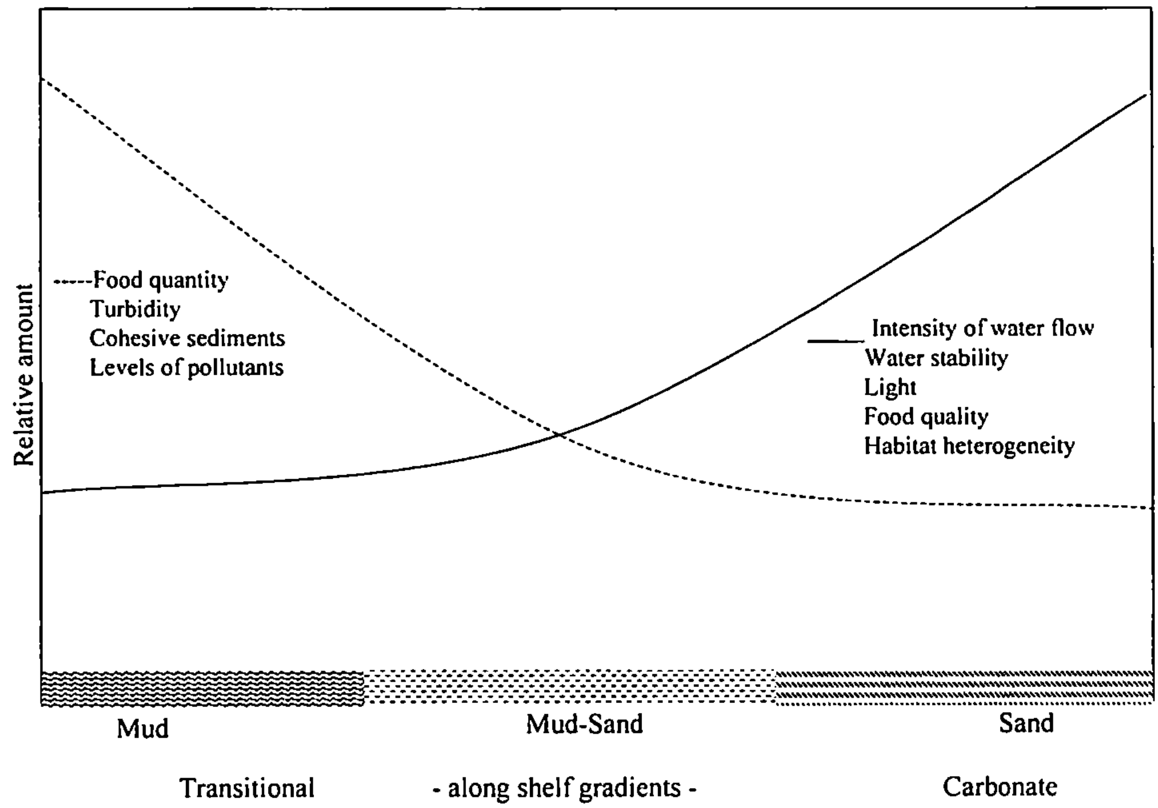


Figure 5.7. Schematic representation of environmental gradients of sediment type, water movement and related variables along the Southern GoM continental shelf.

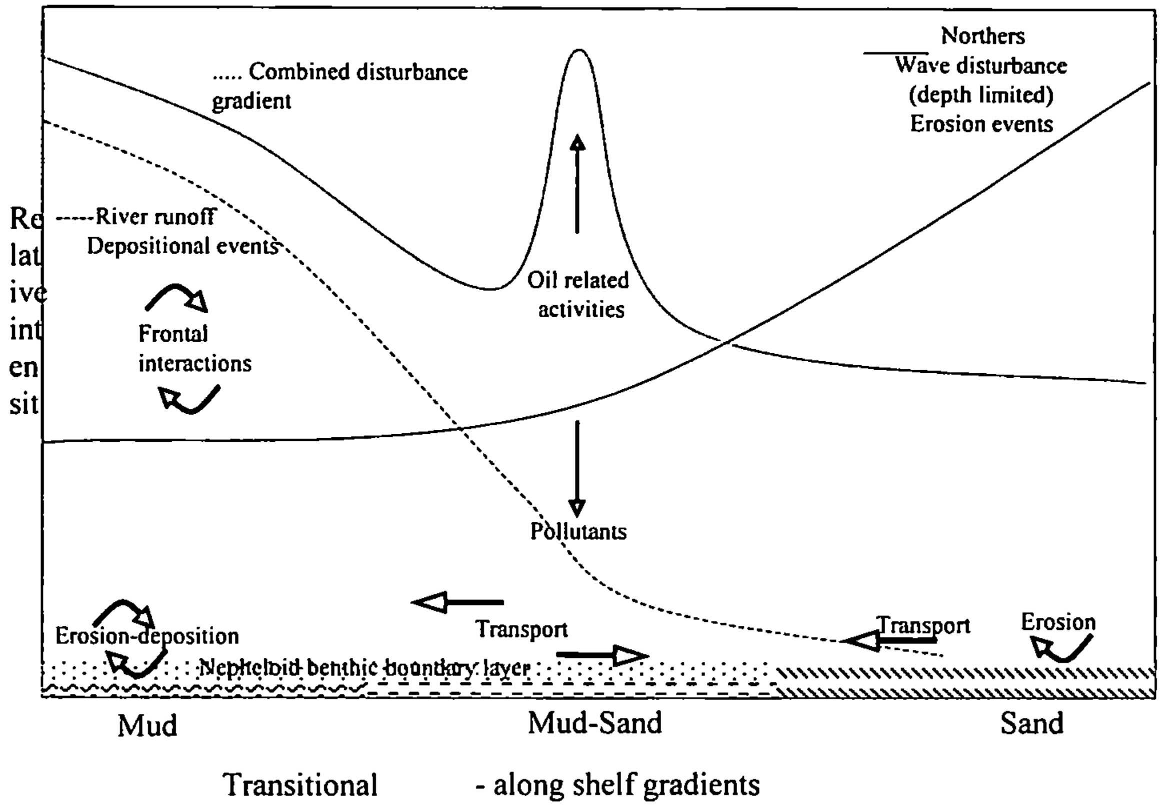


Figure 5.8. Schematic representation of natural and anthropogenic disturbance gradients and how they influence the sedimentary environments as a consequence of water movement along the Southern GoM continental shelf.

These environmental gradients are tightly coupled to the disturbance regime (Figure 5.8). The transitional shelf is subject to river runoff and related depositional events, followed by winter storms. Storms disturbance effect on the sea bed is damped by the cohesive properties of the sediment, that would result in a nepheloid benthic boundary layer that can be dispersed over large areas (McGrail & Carnes 1983, Rezak *et al.* 1985). Frontal interactions between fresh and oceanic water generate small-scale cyclonic and anti-cyclonic circulation (Carranza-Edwards *et al.* 1993). Additional potential impacts come from the oil-related activities, which contribute to an increased load of pollutants that would be further dispersed within the fluid benthic boundary layer (see Chapter 4 and Rosales-Hoz *et al.* (1994), Macias-Zamora *et al.* (1999), Rosales-Hoz *et al.* (1999)). The combined effect of disturbance is thus greater on the transitional shelf than on the carbonate shelf, which is subjected only to periodic winter storms, and resulting wave disturbance and erosional events (Logan *et al.* 1969, Fiers 1996).

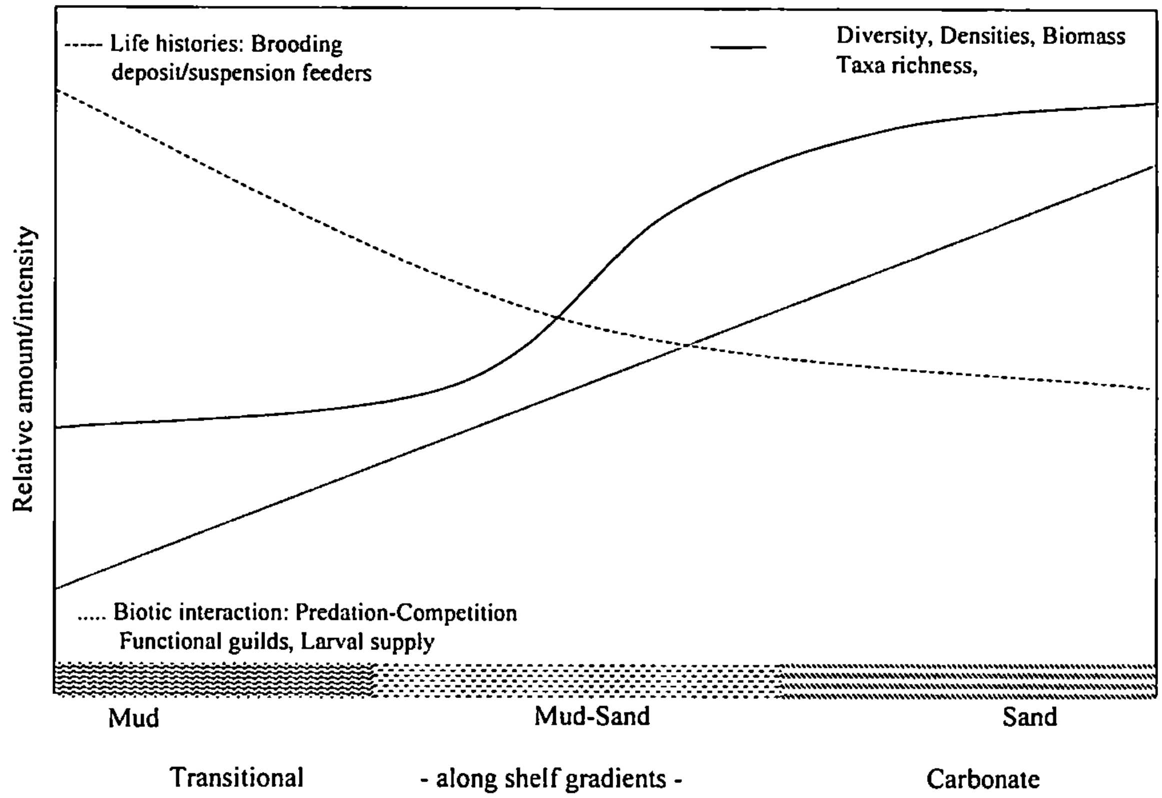


Figure 5.9. Schematic representation of the biological response to the overall disturbance gradients along the Southern GoM continental shelf.

These environmental gradients and disturbance regimes shape benthic community structure through interactions with life histories and population dynamics of macroinfauna (Zajac *et al.* 1998), specifically species response to disturbance (Grassle & Sanders 1973, Moverley *et al.* 1986, Pearson *et al.* 1986, Peterson & Black 1988, Beukema *et al.* 1996, Armonies *et al.* 2001). In the Southern GoM this interaction produces a large-scale pattern of biological response (Figure 5.9) where carbonate sediments harbour a richer and denser macroinfauna community than soft muddy environments (Table 1). The pattern is similar to carbonate and terrigenous shelves of the northern Gulf (Flint & Rabalais 1981, Phillips *et al.* 1990, Posey *et al.* 1998).

The life history of opportunistic taxa provides an example of reproductive modes adapted to disturbance. (Barry 1989) reported that the reproductive response of *Phragmatoma lapidosa californica* (a gregarious, sedentary, tube building polychaete) to disastrous wave disturbance events was the release of gametes into the water column. High densities of sedentary polychaetes (Sabellidae and Serpulidae) and superficial burrowing polychaetes (Spionidae, Paraonidae) were observed on the Campeche Shelf after 4 months of the 'northers' season (see Chapter 2), but whether this response is a reproductive adaptation remains to be determined. Similarly, (Santos & Simon 1980) noted that following annual disturbance by hypoxia, the dominant species in a Florida estuary had adaptations of brood protection (e.g *Ampelisca abdita*) and good dispersal ability either as larvae, juveniles or adults. Brood protection was observed in tanaids (Parapseuidae) and amphipods that attained high densities in the inner shelf of the transitional region 4 months after the rainy season and ostracods from a few sites within the area of oil activities. The link between increases in densities of several macrofaunal families in the Campeche Shelf and such disturbance events, is supported by the synchronised response along and across the shelf (Beukema *et al.* 1996). (Gray 1979) has postulated that, at increasing levels of disturbance, brooding species will have the advantage in terms of colonising vacant niches, assuming there is an adult population (e.g. tanaids see chapter 2 and 3, SIMPER analyses).

Biotic interactions contribute to the shaping of community structure at smaller spatial scales through interactions such as facilitaton, inhibition and tolerance (Rhoads & Young 1970, Eckman *et al.* 1981, Nowell *et al.* 1981, Gallagher *et al.* 1983, Zajac *et al.* 1998). Although the scale of observation and resolution of analyses in this study do not provide much direct information about biotic interactions, it is proposed that there might be a decrease in intensity of biological interactions from the carbonate towards the transitional shelf and from shallow to deeper areas (Figure 5.9). There is a general view that muddy environments will support higher densities of infauna as they contain relatively large amounts of organic matter (Gray 1974, Rhoads & Boyer 1982). However, muddy environments can also present a difficult environment because of changes in oxygen and water chemistry as a result of high organic content, which can lead to hypoxia, or the low quality of food in areas of river deposition. This stressful environment will result in a naturally impoverished area (e.g. the transitional shelf) where low densities will diminish biotic interactions.

Another general observation from the transitional shelf that also hints at a loose biotic interaction pattern is the near absence of sabellids (suspension feeding polychaetes, Chapter 2). The observation seems to support the general thrust of the Trophic Group Amensalism hypothesis (Rhoads & Young 1970). However, following the criticisms of (Hall 1994, Wildish & Kristmanson 1997), this is more likely to be the result of disturbance related to sediment transport, deposition from river influence and bottom current patterns (Chapter 3). The observation is perhaps better explained by the Trophic Group Mutual Exclusion model, which predicts that erosional environments will harbour a mixed community of several feeding modes, and suspension feeders will be excluded from quiescent areas (Wildish & Kristmanson 1997).

The carbonate part of the Campeche Shelf is considered an erosional environment affected by tractive currents from the Yucatan current (Logan *et al.* 1969, Fiers 1996). These erosional events are accentuated during winter storms, where wave stress can influence the bed at the shelf break (Logan *et al.* 1969). Community composition here is more diverse and composed of various feeding modes including suspension feeders, scavengers/predators and deposit feeders (Chapter 2). In contrast, the transitional shelf is a depositional environment from the discharging rivers but also due to advected fine material from the carbonate shelf, as indicated by the high carbonate content of its sediment. Thus, the exclusion of obligate suspension feeders from the transitional shelf could be related to a combination of the fluid constituency of the muddy environment and erosional and depositional events from river runoff and winter storms. However, facultative suspension feeders can thrive in these conditions, attaining high densities (e.g. Spionidae polychaetes and Parapseudidae tanaids) by exploiting changes in water flow and food supply (Fauchald & Jumars 1979, Lopez & J.S.Levinton 1987, Hentschel 1998, Pearson 2001).

Conclusion

This hierarchical and integrative approach to community succession and structure, considers disturbance as the controlling mechanism, which either constitutes the start or end point in a cycle of mosaics of soft bottom benthic community structure (Reise 1991). 'Northers' are considered the common environmental factor that operate over a large scale as noted from the synchronised response of macroinfauna across the whole shelf. At a smaller scale other factors are superimposed, e.g. river runoff and oil-related disturbance. (Alongi 1990), in his review of tropical soft bottom ecosystems noted, that disturbance from heavy rainy seasons and river runoff, storms, mixed carbonate-terrigenous sedimentary facies and high temperatures all play an important role in structuring benthic communities. Thus, the Campeche Shelf represents a typical tropical environment where climatic disturbance is mirrored by the spatial and temporal structure of the benthic infauna and constitutes the driving mechanism of benthic community structure and succession. Within this general pattern of a naturally disturbed environment, the influence of oil-related activities was still apparent due to increases in variability in community composition.

Table 5.1. Density and biomass (gc-grams of carbon, AFWD- ash free weight dry, gww-grams of wet weight) of macroinfauna from continental shelves around the world compared to that found in the southern GoM.

Locality	Depth (m)	Sediment type	Sieve (mm)	Mean density (Range)	Mean biomass (range)	Disturbance	Reference
Gulf of Mexico							
Texas inner shelf	15-21	Silt-clay to muddy-sand	0.5	250-5 250 temporal 2y		Seasonal hypoxia	Harper et al., (1981)
Southern Texas	10-133	Silt-clay to muddy-sand	0.5	1670-27260		Winter storms	(Flint & Rabalais 1981)
North-east Florida-Alabama	75-189		0.5	754 (133-1946)	3.5 (0.7-7.2) (gc)		(Blake & Doyle 1983)
North-western	Mean 20		0.5	8637-18437 730-1346	1.3-1.5 (gc) 0.1-0.2 (gc)	Seasonal hypoxia	(Rabalais *et al.* 1999)
Western	16-120	Mud		36-71	0.9-1.6 (gc)	River runoff	(Escobar and Quintana, 1994 in Rabalais *et al.* 1999)
Western	16-206	Mud		22-125	0.78-2.4 (gc)	River runoff	(Escobar-Briones & Soto 1997)
Southwest Florida Shelf	10-160	Sand to coarse silt	0.5	1 280-14 202			(Phillips *et al.* 1990)
Cedar key Florida Shelf	13	Sand	0.5	1 110-1 785		Tropical storm	(Posey *et al.* 1996)
Campeche Shelf	20-100	Carbonate sandy-mud to sand	1.0 0.5	180-1 296 (spring) 314-614 (winter)	1.6-25 spring 5.1-60.2 winter (gww)	Northers	Spichak and Formoso, (1974)
	35	mud	0.5	1 280-15 620 (m3)		Natural oil seep	Gonzalez-Macias, (1983)
	23-170	Sand to muddy-sand Carbonate-terrigenous	1.0	1634 (120-4540) March 6260 (860-18440) June 8034 (680-27480) Oct			Hernandez-Arana Chapter 2

Table 5.1. Density and biomass (gc-grams of carbon, AFWD- ash free weight dry, gww-grams of wet weight) of macroinfauna from continental shelves around the world compared to that found in the southern GoM.

Locality	Depth (m)	Sediment type	Sieve (mm)	Mean density (Range)	Mean biomass (range)	Disturbance	Reference
Campeche Shelf	15-135	Muddy	0.5	1240 (100-4300)	3.04 (0.1-4.0) (gww)	River runoff	Hernandez-Arana Chapter 3
		Muddy		3580 (200-35800)	5.54 (0.2-57.7) (gww)	winter storms	
NE Atlantic							
Georges Bank region	60-200	Sand to mud	0.3	(3150-30000) Temporal 2y		Winter storms	(Maciolek & Grassle 1987)
	50-200	Coarse sand to coarse silt	0.5	(1000-40000) Temporal 1y		Winter storms	(Michael 1987)
	25-250	Sand to mud	1.0	(<1000 – 26208)	<50-5 246 gww	Winter storms	(Theroux & Grosslein 1987)
Caribbean Sea							
Golfo Triste Venezuela	7-25	fine sands	0.5	3303 (1452-7275)			(Bone & Klein 2000)
North Sea							
Northumberland coast	80	Fine sandy-silt	0.5	830-1067 temporal, 1y			Buchanan and Warwick, (1974)
Skagerrak NE Atlantic	65-100	Sandy-mud to muddy-clay	0.5	(1400-11930)	210-710 gww		(Rosenberg 1995)
North western	50-150	Silt to sand	0.5	250-2500			(Basford *et al.* 1996)
North Sea	20-270	Fine sands to medium silts	0.5	(2361-21153)	1.8-38.1 AFDW		(Dauwe *et al.* 1998)
Mediterranean Sea							
Cretan Shelf	40-190	Sand to silt-clay	0.5	663-4248	0.35-1.46 AFDW		(Karakassis & Eleftheriou 1997)
Ligurian Shelf	5-135	Fine sand to coarse silt	0.5	306-2540	173-1789 AFDW	River runoff	(Albertelli *et al.* 1999)

Table 5.1. Density and biomass (gc-grams of carbon, AFWD- ash free weight dry, gww-grams of wet weight) of macroinfauna from continental shelves around the world compared to that found in the southern GoM.

Locality	Depth (m)	Sediment type	Sieve (mm)	Mean density (Range)	Mean biomass (range)	Disturbance	Reference
Australia							
Victoria	11-51	Medium to coarse sand	0.5	5800 (330-28240)			(Coleman *et al.* 1997)
Central GBR	15-46	terrigenous-carbonate	0.5	3056 (2060-5406)	0.94-3.37 AFDW	River influence and storms	(Alongi 1989a)

APPENDIX

Appendix 1

Summary of location, depth, organic matter and sediment characteristics of stations sampled in the carbonate and transitional shelf of the Southern Gulf of Mexico after the 'northers', dry and rainy seasons of 1993.

a) 'Northers' season March 1993

Station	Latitude N	Longitude W	depth (m)	Organic matter (%)	sand	silt	clay	mean (μm)	sorting
A1	21.5163	92.4339	170	0.79	46.88	29.30	23.82	17.19	4.90
A1	21.5163	92.4339	170	0.83					
A1	21.5163	92.4339	170	0.77					
A2	20.9867	92.3997	80	0.73	13.06	72.42	14.52	8.23	3.10
A2	20.9867	92.3997	80	0.79					
A2	20.9903	92.3957	80	0.58					
A3	20.3991	92.3703	144	1.26	2.47	53.60	43.93	1.71	3.08
A3	20.3993	92.3701	144	1.23					
A3	20.3993	92.3701	144	1.17					
F	20.1825	92.1193	104	0.97					
F	20.1825	92.1193	104	1.07	3.19	44.71	52.10	1.00	3.44
F	20.1825	92.1193	104	1.07					
A5	19.4135	92.5013	117	1.05	1.62	34.11	64.27	0.43	3.70
A5	19.4103	92.4985	117	0.97					
A5	19.4103	92.5152	117	1.04					
B1	21.4125	91.8299	50.8	0.45	56.92	38.52	4.56	74.82	2.67
B1	21.4126	91.8293	51.2						
B1	21.4121	91.8301	51						
B2	20.7452	91.8488	45.1	0.57	22.30	70.44	7.26	23.47	2.67
B2	20.7452	91.8488	45.1	0.58					
B2	20.7452	91.8488	45.1	0.36					
B3	20.3485	91.7181	42	0.63	18.27	70.89	10.85	16.29	3.29
B3	20.3485	91.7181	42	0.77					
B3	20.3357	91.7171	42	0.72					
B4	20.1821	91.8868	44.5	0.56	30.37	55.84	13.79	17.28	3.60
B4	20.1821	91.8868	44.5	0.66					
B4	20.1821	91.8868	44.5	0.92					
B5	20.1170	91.7451	38.5	0.88	12.83	73.10	14.07	9.88	3.09
B5	20.1170	91.7451	38.5	0.96					
B5	20.1170	91.7451	38.5	1.09					
B6	19.7529	91.8359	48.4	0.58	78.93	8.40	12.67	101.03	4.29
B6	19.7529	91.8359	48.4	0.47					
B6	19.7529	91.8359	48.4	0.64					
B7	19.4205	91.8393	39.5	0.98	4.19	61.13	34.68	1.89	3.23
B7	19.4205	91.8393	39.5	1.22					
B7	19.4205	91.8393	39.5	1.02					
B8	19.1598	91.9856	23	0.54					
B8	19.1598	91.9856	23	0.65	7.93	73.46	18.60	10.23	3.54
B8	19.1598	91.9856	23	0.5					

Appendix 1. (continued)

b) Dry season June 1993

Station	Latitude N	Longitude W	depth (m)	Organic matter (%)	sand	silt	clay	mean (μm)	sorting
A1	21.5160	92.4425	178	0.84	32.39	10.78	56.83	2.18	5.81
A1	21.5146	92.4525	185.3	0.71					
A1	21.5160	92.4388	174.9	0.79					
A2	20.9828	92.4069	77.2	0.74	8.79	82.55	8.66	11.17	4.82
A2	20.9824	92.4122	77.8						
A2	20.9669	92.4169	78.4	0.73					
A3	20.5770	92.3724	93.1	0.87	56.09	27.46	16.46	43.52	4.87
A3	20.5778	92.3757	101.8	0.85					
A3	20.5798	92.3834	256	1.22					
F	20.1861	92.1229	106.7	1.22					
F	20.1877	92.1274	109.2	1.25	0.99	48.00	51.01	1.59	2.58
F	20.1849	92.1189	104.7	1.25					
A5	19.4183	92.5121	123.5	1.14	2.21	8.03	89.75	0.13	3.31
A5	19.4189	92.5180	123.8	1.14					
A5	19.4201	92.5252	125.6	0.99					
B1	21.4102	91.8443	51.4	0.31					
B1	21.4072	91.8494	51	0.41					
B1	21.4014	91.8618	51.6	1.06	52.00	39.90	8.10	82.03	3.31
B2	20.7415	91.8576	44.9	0.55					
B2	20.7384	91.8635	44.6	0.52					
B2	20.7367	91.8666	45.3						
B3	20.3350	91.7224	41	0.83					
B3	20.3356	91.7242	40.1	0.84	10.53	81.90	7.57	13.90	2.69
B3	20.3371	91.7321	41.3	0.67					
B4	20.1840	91.8859	47.4	0.74	2.85	41.96	55.19	1.61	2.99
B4	20.1843	91.8910	47.2	0.83					
B4	202.3833	91.8964	47.1	0.77					
B5	20.1166	91.7365	40.9	1	11.71	25.34	62.95	0.82	4.97
B5	20.1159	91.7403	41.7	1.06					
B5	20.1159	91.7434	41.5	0.56					
B6	19.7516	91.8377	50.1	0.83	62.75	18.04	19.21	36.31	4.84
B6	19.7500	91.8447	49.4	0.42					
B6	19.7498	91.8358	49.4	0.59					
B7	19.4169	91.8389	40.3	1.39	3.13	48.03	48.84	1.86	2.65
B7	19.4143	91.8389	40.6	1.39					
B7	19.4132	91.8465	40.2	1.39					
B8	19.1474	91.9939	22.5	0.61	5.62	86.92	7.46	13.63	2.51
B8	19.1462	91.9984	22.2						
B8	19.1522	91.9862	22.2	0.65					

Appendix 1. (continued)

c) Rainy season October 1993

Station	Latitude N	Longitude W	depth (m)	Organic matter (%)	sand	silt	clay	mean (µm)	sorting
A1	21.4992	92.4458	179	0.81	34.41	33.00	32.59	7.02	5.01
A1	21.5244	92.4296	166	0.85					
A1	21.5311	92.4281	166	0.72					
A2	20.9827	92.3983	73.3	0.82	11.32	61.00	27.45	7.64	4.06
A2	20.9809	92.3975	73.8	0.81					
A2	20.9792	92.3983	72.5	0.66					
A3	20.5638	92.3676	122.9	1.12	2.73	45.00	52.30	10.15	4.06
A3	20.5684	92.3656	89.1	1.09					
A3	20.5674	92.3691	125.6	1.22					
F	20.1871	92.1166	100	1.22					
F	20.1879	92.1199	101	1.18	2.38	42.33	55.22	10.62	3.55
F	20.1880	92.1215	102	1.19					
A5	19.4148	92.4869	118	1.14	1.59	6.83	91.56	12.90	3.27
A5	19.4147	92.4766	116	1.2					
A5	19.4166	92.4684	115	1.18					
B1	21.4069	91.8431	47.8	0.33	83.76	10.17	6.08	2.83	3.48
B1	21.4110	91.8242	45.1	0.47					
B1	ns	ns							
B2	20.7464	91.8402	42.7	0.53	29.12	53.83	17.37	5.74	3.44
B2	20.7463	91.8398	42.8	0.56					
B2	20.7463	91.8392	41.4	0.56					
B3	20.3326	91.7176	38.1	0.76					
B3	20.3283	91.7127	37.1	0.76					
B3	20.3241	91.7093	37.2	0.72	10.67	78.60	10.72	6.26	3.06
B4	20.1820	91.8822	42.3	0.76	35.23	53.70	11.09	5.48	3.74
B4	20.1797	91.8740	43.1	0.85					
B4	20.1786	91.8814	43	1.06					
B5	20.1188	91.7354	37.7	1.03	15.97	76.83	7.27	6.11	2.97
B5	20.1188	91.7348	37.1	1					
B5	20.1190	91.7361	39.2						
B6	19.7489	91.8340	46.4	0.35	41.75	28.80	32.11	6.86	4.67
B6	19.7503	91.8201	48.2	0.93					
B6	19.7491	91.8295	48.3	0.82					
B7	19.4122	91.8243	36.1	1.37					
B7	19.4097	91.8152	36.5	1.3	3.42	27.67	69.16	11.42	3.54
B7	19.4051	91.8067	35.5	1.27					
B8	19.1455	91.9815	19.5	0.54	1.41	72.83	25.74	7.50	3.85
B8	19.1413	91.9741	19	0.54					
B8	19.1351	91.9679	19.3	0.5					

Appendix 2.

Summary of number of families (S), number of individuals (N), Shannon diversity index log*e* (H') of macroinfauna per 0.05 m^2 at each Transect-Station-Replicate (TSR) sampled during three seasons in 1993 in the Southern Gulf of Mexico. * Stations used for the ANOVA analysis, ns (not sampled stations).

	Northers March 1993			Dry June 1993			Rainy October 1993		
TSR	**S**	**N**	**H'**	**S**	**N**	**H'**	**S**	**N**	**H'**
A11	24	48	3.0	31	126	2.7	24	105	2.8
A12	20	37	2.8	30	214	2.7	32	90	3.0
A13	15	16	2.7	22	97	2.6	25	107	2.5
*A21	6	6	1.8	42	142	3.3	50	429	3.2
*A22	23	45	2.9	49	181	3.4	49	418	3.2
*A23	13	23	2.4	46	255	3.1	46	322	3.1
*A31	17	38	2.7	31	254	3.0	26	159	2.6
*A32	18	33	2.8	34	111	3.2	43	206	3.4
*A33	16	42	2.6	ns	ns	ns	29	211	2.5
*A41	13	19	2.5	22	80	2.8	24	83	2.9
*A42	14	32	2.4	24	90	2.8	25	65	2.9
*A43	10	27	1.9	ns	ns	ns	31	66	3.2
*A51	11	19	2.3	17	43	2.6	27	56	3.1
*A52	14	21	2.5	24	59	2.9	16	34	2.6
*A53	12	14	2.4	28	71	3.0	26	81	2.9
B11	ns	ns	ns	19	83	2.5	46	195	3.1
B12	ns	ns	ns	30	311	2.6	54	922	2.7
B13	ns	ns	ns	58	685	3.0	ns	ns	ns
*B21	33	118	3.1	42	806	2.7	49	859	2.7
*B22	31	122	3.0	53	799	2.7	49	1041	2.8
*B23	39	239	3.0	53	922	2.9	49	980	2.7
B31	35	174	3.0	41	662	2.6	35	391	2.7
B32	35	215	2.9	41	780	2.6	31	405	2.8
B33	28	123	2.8	45	416	3.0	55	1006	2.7
*B41	30	110	3.0	47	687	2.6	56	1116	3.1
*B42	33	112	3.0	40	580	2.7	48	1374	2.9
*B43	34	126	3.1	39	251	3.0	50	1160	2.7
B51	31	111	2.9	22	91	2.5	12	144	1.3
B52	19	86	2.2	30	268	2.6	32	310	2.2
B53	17	61	2.3	31	280	2.4	26	240	2.1
B61	38	218	3.0	41	306	2.9	55	786	2.9
B62	44	227	3.2	35	171	2.8	37	187	2.8
B63	36	210	3.1	41	349	2.9	43	304	3.2
*B71	18	35	2.8	24	154	2.4	15	54	2.3
*B72	13	26	2.5	19	115	2.1	18	71	2.3
*B73	11	18	2.3	27	187	2.7	16	46	2.4
*B81	19	57	2.4	25	225	2.1	32	211	2.6
*B82	16	71	2.3	24	192	2.4	30	469	2.3
*B83	19	61	2.4	32	537	2.2	37	563	2.6

Appendix 3.

Appendix 3a) Summary of location, depth, distance to the nearest oil field, bottom salinity, organic matter and carbonate content of sediments of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Rainy season of 1999.

TS	Latitude N	Longitude W	Depth m	Nearest oil field km	Salinity UPS	Organic matter (%)	Carbonate (%)
A1	18.9783	91.9232	19	30	34.9728	4.5	59.3
A2	19.0453	91.968	21	22.5	35.5656	6.9	53.5
A3	19.0808	92.0192	22	15	35.5521	3.3	60.6
A4	19.1322	92.061	23	7.5	35.2873	3.8	61.4
A5	19.1835	92.1185	25	4.4	35.3945	4.2	58.6
A6	19.234	92.1667	31	1.3	35.467	8.8	54.5
A7	19.2852	92.2185	38	1.3	36.1174	14.0	42.4
A8	19.3326	92.2674	46	3.8	36.1126	9.5	38.7
A9	19.3834	92.3189	63	2.5	36.303	9.2	36.1
A10	19.4335	92.3676	93	2	36.2983	13.0	34.0
A11	19.4803	92.4197	116	6.3	36.3787	10.0	34.0
A12	19.5292	92.4679	135	13.8	36.3424	9.5	30.5
B1	19.0499	91.7851	12	33	35.6323	3.2	75.0
B2	19.1006	91.835	15	25.5	35.5878	4.6	58.5
B3	19.1488	91.8854	22	16	35.6215	1.8	64.7
B4	19.2022	91.9356	23	10	35.7113	5.0	64.5
B5	19.2518	91.9857	27	2.5	35.433	7.2	62.9
B6	19.3014	92.0359	34	3.8	35.54	7.8	54.0
B7	19.351	92.0858	41	2.5	36.1576	9.0	36.6
B8	19.4006	92.1358	45	5.8	36.1525	9.9	35.7
B9	19.4494	92.1852	52	2.5	36.2623	13.2	34.6
B10	19.5007	92.2322	60	3.2	36.2597	11.5	48.4
B11	19.5514	92.2857	87	5	36.141	12.7	42.8
B12	19.6014	92.3353	112	10	36.334	3.9	32.5
C1	19.0987	92.4342	37	15	36.1089	12.0	31.0
C2	19.1337	92.3668	35	6.3	36.03	7.7	40.7
C3	19.1658	92.3005	32	2	35.9761	8.7	40.9
C4	19.1994	92.2341	32	1.3	35.4931	8.6	46.2
C5	19.2317	92.169	30	1.3	35.6582	7.5	53.2
C6	19.2667	92.1029	32	2.5	35.4919	8.6	51.9
C7	19.3013	92.0365	34	3.8	35.9468	9.0	51.6
C8	19.303	91.9687	36	3.8	36.0939	9.2	50.1
C9	19.3677	91.9026	38	11	35.821	10.7	47.6
C10	19.403	91.8357	39	16	35.8454	13.9	48.2
C11	19.4339	91.7677	39	21.5	35.9196	8.2	54.9
C12	19.4658	91.7024	39	28	35.9745	8.4	56.1
D1	19.2337	92.4669	67	16.3	36.2086	16.4	25.9

Appendix 3a. (Continued)

TS	Latitude N	Longitude W	Depth m	Nearest oil field km	Salinity UPS	Organic matter (%)	Carbonate (%)
D2	19.2665	92.401	52	8.8	36.1794	8.2	31.0
D3	19.301	92.3365	51	2	36.1768	12.8	33.5
D4	19.3339	92.2682	46	3.8	36.201	6.0	36.1
D5	19.3689	92.201	46	3	36.2312	9.0	38.3
D6	19.4004	92.1332	45	5.8	36.1779	9.2	44.5
D7	19.4385	92.0723	49	0.7	36.1556	12.7	40.2
D8	19.4637	91.9968	48	3.8	36.1683	13.8	42.9
D9	19.5	91.9328	49	2.5	36.156	7.6	57.9
D10	19.5353	91.8648	49	11.3	35.8837	11.7	50.8
D11	19.5673	91.8007	46	18.8	36.0001	13.6	43.9
D12	19.5988	91.7424	44	26.3	35.9088	8.5	51.9

Appendix 3b) Summary of measurements of sediment structure and composition of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Rainy season of 1999.

TS	Sand (%)	Silt (%)	Clay (%)	Surface area ($m^2\,gm^{-1}$)	Moment mean (phi)	Moment stdev.(phi)
A1	10.7	80.5	8.75	0.4889	6.07	1.99
A2	3.85	85	11.2	0.5457	6.82	1.76
A3	25.1	69.5	5.41	0.3072	4.96	2.13
A4	23.7	69.6	6.76	0.3791	5.13	2.56
A5	7.3	83.9	8.76	0.4827	6.04	1.91
A6	2.31	85.9	11.8	0.6463	6.83	1.78
A7	0.83	85.1	14.1	0.6803	7.28	1.56
A8	1	84.1	14.9	0.7008	7.34	1.57
A9	15.9	68.6	15.5	0.7634	6.38	3.28
A10	2	80.6	17.5	0.8453	7.48	1.72
A11	1.99	78.9	19.1	0.8911	7.54	1.86
A12	2.29	78.2	19.6	0.8975	7.54	1.78
B1	8.6	86	5.36	0.3503	5.5	1.68
B2	21	70.3	8.76	0.4288	5.68	2.35
B3	14.3	77.7	8.05	0.4546	5.79	2.01
B4	24.4	72.9	2.68	0.1535	4.79	1.45
B5	9.22	83.8	7.04	0.4074	5.67	1.85
B6	1.77	86.5	11.7	0.6473	6.87	1.74
B7	21.1	67.8	11.1	0.5933	6.24	2.47
B8	0.98	83.9	15.1	0.7855	7.35	1.64
B9	0.69	83.4	15.9	0.7388	7.43	1.55
B10	1.17	81.4	17.4	0.8529	7.49	1.7
B11	1.23	81.1	17.7	0.8457	7.51	1.69
B12	2.6	78	19.4	0.8327	7.55	1.82

Appendix 3b. (Continued)

TS	Sand (%)	Silt (%)	Clay (%)	Surface area ($m^2 gm^{-1}$)	Moment mean (phi)	Moment stdev.(phi)
C1	2.78	84.5	12.7	0.6553	7.01	1.74
C2	1.14	83.7	15.1	0.7724	7.28	1.68
C3	0.94	86	13.1	0.6998	7.18	1.62
C4	1.25	85.9	12.8	0.6962	7.08	1.67
C5	1.88	86.9	11.2	0.557	6.87	1.66
C6	1.85	85.8	12.3	0.6679	6.9	1.77
C7	1.59	85.6	12.8	0.6941	7.02	1.73
C8	1.27	86.2	12.5	0.6243	7.07	1.64
C9	0.8	83.7	15.5	0.81	7.34	1.66
C10	0.99	84	15	0.7966	7.32	1.68
C11	1.5	83.8	14.7	0.7739	7.31	1.72
C12	1.15	85	13.9	0.6702	7.27	1.58
D1	2.03	83	15	0.7572	7.34	1.72
D2	2.59	82.1	15.3	0.7718	7.3	1.8
D3	0.84	83.3	15.9	0.8131	7.39	1.65
D4	0.7	84.6	14.7	0.7648	7.35	1.6
D5	1.67	83.4	14.9	0.7672	7.29	1.7
D6	1.01	84	15	0.774	7.34	1.64
D7	0.68	84.1	15.3	0.7907	7.39	1.61
D8	1.48	82.6	15.9	0.816	7.39	1.68
D9	1.39	82.6	16	0.8233	7.38	1.69
D10	9.68	77.6	12.7	0.5971	6.78	2.12
D11	2.65	83.1	14.3	0.6776	7.22	1.68
D12	6.71	79.8	13.5	0.7134	6.98	2.01

Appendix 3c) Summary of concentrations (µg/g of dry sediment) of petroleum hydrocarbons and trace metals in sediment of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Rainy season of 1999. TS (transect/station), TH (total hydrocarbons), Tal (total aliphatic), Tar (total aromatic), UCM (unresolved complex mixture)

TS	TH	TAl	TAr	UCM	Fe	Mn	Zn	Cu	Cr	Ba	Ni
A1	1.40	1.26	0.14	1.26	6430	130.51	15.73	nd	9.82	12.68	88.68
A2	0.36	nd	0.36	nd	7673	145.47	18.60	nd	11.98	14.62	116.49
A3	0.36	nd	0.36	nd	5856	119.09	14.08	nd	9.84	17.96	72.65
A4	0.17	nd	0.17	nd	6126	128.43	14.86	nd	9.93	23.47	91.59
A5	0.10	0.01	0.09	nd	7046	156.47	17.97	2.54	10.46	143.30	102.69
A6	0.08	0.02	0.06	nd	8658	199.68	25.96	3.70	14.53	446.40	125.82
A7	63.56	32.68	30.89	63.45	11633	259.62	35.66	5.28	18.11	431.81	115.03
A8	36.79	21.56	15.22	36.45	12704	294.18	42.13	5.59	20.22	368.28	89.13
A9	18.62	9.51	9.11	18.38	14741	361.50	54.55	6.14	20.98	217.48	113.39
A10	14.85	9.51	5.34	14.83	15403	381.31	48.67	6.69	16.73	144.99	180.08

Appendix 3c. (Continued)

TS	TH	TAl	TAr	UCM	Fe	Mn	Zn	Cu	Cr	Ba	Ni
A11	6.13	4.69	1.44	5.93	15638	342.83	50.08	7.83	17.21	62.10	132.76
A12	5.59		5.59	5.16	17286	326.77	66.91	8.71	17.52	55.52	160.53
B1	11.32	4.91	6.41	10.83	3746	78.36	8.31	nd	6.11	7.06	101.01
B2	12.78	5.63	7.15	12.36	7331	141.34	17.25	nd	10.19	12.48	110.35
B3	1.45	1.09	0.36	1.08	6233	122.92	14.02	nd	8.77	11.38	142.83
B4	14.23	10.47	3.76	14.15	6607	130.12	20.48	nd	8.03	36.14	148.40
B5	3.39	1.22	2.17	2.98	7316	154.30	20.17	nd	9.73	245.73	158.04
B6	24.62	17.24	7.38	24.27	11352	251.20	40.32	4.05	18.30	244.27	181.84
B7	37.21	30.26	6.95	37.02	12742	266.28	38.23	4.77	20.82	358.83	78.87
B8	114.37	73.81	40.55	113.59	12999	294.05	38.99	5.03	20.17	303.56	93.18
B9	96.81	43.82	52.99	96.56	14673	318.07	43.08	5.64	20.56	269.95	68.20
B10	34.18	15.38	18.80	33.66	18091	427.94	54.35	7.03	23.75	234.99	103.78
B11	24.73	14.47	10.26	24.34	16538	385.03	47.88	7.38	19.23	184.76	143.08
B12	15.57	6.76	8.80	14.82	13436	375.14	46.44	6.25	14.07	64.36	127.81
C1	18.60	10.17	8.43	18.18	14331	306.06	42.05	6.14	19.73	96.33	123.01
C2	26.26	17.68	8.58	26.07	13555	281.76	38.30	5.47	21.37	84.05	59.39
C3	22.81	12.04	10.77	22.47	11658	261.06	34.10	4.60	18.68	227.62	129.78
C4	48.33	38.31	10.02	46.34	11854	271.62	34.10	4.78	17.33	356.94	130.96
C5	25.66	18.71	6.95	25.46	10090	203.23	25.44	4.08	19.11	378.56	nd
C6	17.48	8.93	8.55	16.94	10704	209.53	26.46	3.74	18.81	120.78	120.86
C7	11.16	8.92	2.24	10.93	9669	203.41	26.40	3.35	15.37	229.05	150.74
C8	30.28	30.16	0.12	29.21	9408	216.72	28.93	nd	15.75	160.02	142.54
C9	48.54	17.21	31.33	48.11	10317	197.51	30.67	3.66	18.11	170.36	84.16
C10	28.23	24.37	3.86	27.96	10392	186.34	29.78	3.71	17.91	143.54	77.18
C11	8.09	3.19	4.90	7.49	8801	161.64	23.25	2.98	15.47	47.07	nd
C12	49.23	43.88	5.36	48.65	9210	168.74	24.53	3.25	16.76	33.34	121.96
D1	25.46	21.43	4.03	25.30	15018	323.92	43.41	6.66	19.62	179.58	167.78
D2	43.32	31.10	12.22	46.40	13942	311.48	52.25	5.87	19.84	251.35	130.60
D3	60.95	48.52	12.42	60.43	12822	281.70	39.03	5.19	19.41	356.13	93.66
D4	83.38	58.58	24.80	83.14	12674	274.62	38.43	4.93	18.74	296.81	161.51
D5	101.63	65.34	36.29	101.31	12235	258.08	35.86	5.12	19.09	407.90	107.85
D6	41.25	32.95	8.30	40.91	12461	269.84	36.86	4.46	19.42	262.80	163.47
D7	104.75	90.44	14.31	104.29	12569	255.19	42.98	4.80	21.18	422.14	84.48
D8	35.81	32.90	2.91	23.07	11664	232.09	35.93	3.95	18.70	406.73	64.89
D9	16.28	12.91	3.37	16.02	10335	191.50	24.12	3.21	16.22	36.50	64.92
D10	14.42	10.90	3.52	14.18	10580	219.90	27.99	3.59	16.41	115.82	109.71
D11	6.50	5.85	0.65	6.19	12071	243.62	36.49	4.03	18.49	387.34	115.44
D12	29.57	28.37	1.21	11.62	8773	159.00	21.75	2.75	13.98	40.58	105.58

Appendix 4.

Appendix 4a) Summary of location, depth, distance to the nearest oil field, bottom salinity, organic matter and carbonate content of sediments of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Northers season of 1999-2000.

TS	Latitude N	Longitude W	Depth m	Nearest oil field km	Salinity UPS	Organic matter (%)	Carbonate (%)
A1	18.9844	91.9181	19.2	30	36.8279	3.5	53.2
A2	19.0335	91.9665	21.8	22.5	36.7442	2.6	53.4
A3	19.085	92.0179	22.8	15	36.6676	2.7	57.0
A4	19.1328	92.0661	23.5	7.5	36.5913	3.2	61.2
A5	19.1726	92.1122	21	4.4	36.4586	3.1	60.9
A6	19.2337	92.1669	26	1.3	36.5156	7.6	47.3
A7	19.2829	92.2158	34	1.3	36.3006	9.1	39.3
A8	19.3007	92.3302	46.4	3.8	36.2404	6.6	36.7
A9	19.3834	92.3183	60	2.5	36.2141	10.1	34.4
A10	19.4345	92.3683	95	2	36.2767	8.2	29.4
A11	19.4829	92.4153	117	6.3	36.3133	9.0	25.5
A12	19.5353	92.4684	136	13.8	36.2758	11.3	25.0
B1	19.0487	91.7867	18	33	36.7807	2.7	68.3
B2	19.0998	91.8338	21	25.5	36.7144	3.4	56.2
B3	19.198	91.8853	17	16	36.6355	3.5	59.2
B4	19.2009	91.9353	19	10	36.5997	3.4	58.9
B5	19.2508	91.9856	27	2.5	36.5037	4.2	58.8
B6	19.3005	92.0341	29	3.8	36.4755	7.1	51.5
B7	19.3511	92.0838	41	2.5	36.4568	8.9	38.7
B8	19.3994	92.1353	42	5.8	36.4212	8.9	35.6
B9	19.4503	92.1856	54	2.5	36.2714	10.3	33.5
B10	19.5017	92.2334	68.4	3.2	36.1982	9.4	32.0
B11	19.5507	92.284	88	5	36.2529	10.6	28.5
B12	19.6023	92.3397	108	10	36.2907	4.9	27.9
C1	19.0878	92.4335	32	15	37.0664	6.7	33.1
C2	19.1337	92.3671	31	6.3	36.3013	8.9	36.9
C3	19.1671	92.3005	35	2	36.5564	8.5	44.5
C4	19.1979	92.2359	33	1.3	36.5156	9.3	40.0
C5	ns	ns	ns	ns	ns	ns	ns
C6	19.266	92.1019	27	2.5	36.4007	6.3	52.4
C7	ns	ns	ns	ns	ns	ns	ns
C8	19.334	91.9683	33	3.8	36.5589	9.0	49.5
C9	19.3679	91.9001	35	11	36.5128	8.7	48.6
C10			39	16	36.5073	9.1	48.3
C11	19.432	91.7679	39	21.5	36.1724	7.7	50.3
C12	19.466	91.7008	39	28	36.2788	8.6	52.1
D1	19.2342	92.4678	67	16.3	36.2371	9.3	29.5

Appendix 4a. (Continued)

TS	Latitude N	Longitude W	Depth m	Nearest oil field km	Salinity UPS	Organic matter (%)	Carbonate (%)
D2	19.2655	92.401	58	8.8		9.2	30.6
D3	19.3002	92.3353	51	2	36.2602	10.6	34.2
D4	ns	ns	ns	ns	ns	ns	ns
D5	19.3669	92.2024	42	3	36.334	7.1	36.9
D6	ns	ns	ns	ns	ns	ns	ns
D7	19.4329	92.0668	44	0.7	36.9328	9.6	39.3
D8	19.4656	92.0021	45	3.8	36.5175	9.9	40.1
D9	19.4987	91.935	49	2.5	36.616	8.2	43.9
D10	19.5329	91.8683	49	11.3	36.41	7.9	46.1
D11	19.5677	91.7313	52	18.8	36.2421	8.2	57.2
D12	19.5989	91.7313	44	26.3	36.2611	5.8	58.4

Appendix 4b) Summary of measurements of sediment structure and composition of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Northers season of 1999-2000.

TS	Sand (%)	Silt (%)	Clay (%)	Surface area ($m^2 gm^{-1}$)	Moment mean (phi)	Moment stdev.(phi)
A1	8.13	83.4	8.44	0.4708	6.07	1.88
A2	32.1	59.8	8.12	0.429	4.67	3.43
A3	23.5	70.6	5.88	0.3293	5	2.17
A4	14.5	78.2	7.29	0.3996	5.55	1.93
A5	7.45	84.8	7.76	0.4378	5.88	1.87
A6	2	85.6	12.4	0.6637	6.92	1.76
A7	1.59	85.1	13.4	0.7171	7.17	1.67
A8	1.57	81.3	17.1	0.8529	7.37	1.75
A9	1.83	83	15.2	0.7654	7.32	1.73
A10	1.27	79.4	19.3	0.9094	7.54	1.76
A11	1.5	78.8	19.7	0.9033	7.6	1.69
A12	1.81	77.7	20.5	0.846	7.56	1.71
B1	14.8	79.3	5.84	0.3556	5.49	1.82
B2	14.8	77	8.19	0.4027	5.93	2
B3	18.6	74.9	6.49	0.359	5.34	1.97
B4	23.7	69.7	6.6	0.3661	4.93	2.57
B5	7.42	84.2	8.39	0.4665	5.99	1.91
B6	1.61	87.1	11.3	0.622	6.88	1.69
B7	0.89	84.1	15	0.7851	7.3	1.66
B8	1.02	85.8	13.2	0.7036	7.24	1.59
B9	1.17	83.2	15.6	0.7847	7.36	1.65
B10	0.91	82.3	16.8	0.8118	7.47	1.62
B11	2.91	78.3	18.8	0.8683	7.44	1.98
B12	5.12	75.4	19.5	0.8898	7.36	2.24

Appendix 4b. (Continued)

TS	Sand (%)	Silt (%)	Clay (%)	Surface area (m^2 gm^{-1})	Moment mean (phi)	Moment stdev.(phi)
C1	1.64	84	14.4	0.721	7.16	1.72
C2	1.31	84.1	14.6	0.7566	7.22	1.7
C3	0.88	85.2	13.9	0.6662	7.17	1.62
C4	1.39	85.4	13.2	0.707	7.12	1.68
C5	ns	ns	ns	ns	ns	ns
C6	1.86	86	12.2	0.5778	6.9	1.73
C7	ns	ns	ns	ns	ns	ns
C8	4.96	82.6	12.4	0.6629	6.89	1.88
C9	0.93	85.1	14	0.7427	7.23	1.65
C10	1.11	83	15.9	0.8227	7.36	1.69
C11	6.55	79.8	13.7	0.7292	6.86	2.38
C12	3.02	84.5	12.5	0.6866	7.05	1.85
D1	1.44	81.4	17.2	0.8302	7.39	1.73
D2	1.22	81.9	16.9	0.8285	7.4	1.71
D3	0.98	82	17	0.825	7.43	1.68
D4	ns	ns	ns	ns	ns	ns
D5	0.94	82.9	16.1	0.8079	7.37	1.67
D6	ns	ns	ns	ns	ns	ns
D7	0.9	83.9	15.2	0.7745	7.34	1.63
D8	1.21	83.3	15.5	0.7885	7.35	1.66
D9	1.73	82	16.3	0.8207	7.39	1.77
D10	1.32	82	16.7	0.8337	7.4	1.71
D11	6.6	77.8	15.6	0.775	7.06	2.15
D12	8.74	76.6	14.7	0.7504	6.94	2.15

Appendix 4c) Summary of concentrations (µg/g of dry sediment) of petroleum hydrocarbons and trace metals in sediment of sampled stations in the transitional shelf of the Southern Gulf of Mexico after the Northers season of 1999-2000. TS (transect/station), TH (total hydrocarbons), Tal (total aliphatic), Tar (total aromatic), UCM (unresolved complex mixture), nd (not detected)

TS	TH	TAl	TAr	UCM	Fe	Mn	Zn	Cu	Cr	Ba	Ni
A1	7.21	7.15	0.06	7.08	7692	179.89	22.39	nd	11.11	15.37	171.98
A2	15.29	11.05	4.25	15.05	7519	169.57	20.72	nd	10.91	12.38	175.93
A3	8.38	5.04	3.33	8.15	5747	122.31	15.10	nd	8.63	14.15	119.66
A4	6.42	5.30	1.12	6.37	5094	115.17	13.50	nd	7.17	28.25	166.59
A5	20.09	9.02	11.07	19.84	6269	138.11	17.65	nd	9.60	95.08	211.20
A6	24.31	17.79	6.51	24.18	8988	211.48	45.48	3.95	15.21	279.82	179.55
A7	46.17	31.61	14.56	45.94	11451	266.49	38.98	5.12	19.58	369.11	193.93
A8	81.87	57.05	24.83	81.38	11578	295.46	35.55	5.23	19.33	379.88	249.44
A9	47.92	32.38	15.54	47.14	13074	367.79	40.07	5.65	19.00	251.96	260.68
A10	16.12	8.72	7.40	15.47	17385	398.30	50.64	7.83	24.49	41.14	195.76
A11	52.50	23.00	29.50	52.27	13173	378.86	43.18	6.45	13.57	57.18	241.18

Appendix 4c. (Continued)

TS	TH	TAl	TAr	UCM	Fe	Mn	Zn	Cu	Cr	Ba	Ni
A12	3.18	1.32	1.86	3.16	16212	345.74	48.42	7.60	15.66	40.09	236.84
B1	2.57	0.62	1.95	2.42	4364	94.58	7.46	nd	6.60	6.65	282.42
B2	0.02	0.00	0.02	nd	6165	132.06	12.46	nd	7.86	9.75	158.88
B3	6.38	4.45	1.93	6.27	6120	125.05	13.80	nd	8.45	10.85	101.37
B4	1.82	0.03	1.79	1.70	5906	120.93	12.42	nd	7.89	17.10	152.37
B5	0.13	0.01	0.12	nd	6086	138.30	14.53	nd	9.54	147.25	145.22
B6	15.18	9.02	6.16	14.94	9214	216.57	22.64	3.04	14.63	148.32	142.29
B7	67.22	53.56	13.66	50.71	11101	253.97	38.18	4.42	18.48	388.80	177.04
B8	60.41	44.23	16.36	59.73	12239	283.42	35.10	4.77	19.11	293.64	203.50
B9	135.11	80.56	54.55	134.95	13081	315.88	40.73	5.46	19.89	370.74	228.67
B10	95.77	29.19	66.59	95.53	14584	357.66	42.19	5.22	20.32	261.84	284.73
B11	1.05	nd	1.05	1.00	15581	382.97	45.38	6.67	20.58	45.73	187.39
B12	0.65	0.18	0.47	0.27	15143	391.60	47.29	7.36	16.48	24.20	359.30
C1	22.13	15.30	6.83	21.51	16367	361.41	40.71	5.76	22.98	81.58	176.76
C2	14.63	11.46	3.17	13.91	13785	337.84	36.03	5.37	19.94	74.17	334.54
C3	22.83	0.15	22.68	21.93	12192	295.15	32.79	4.35	21.48	154.73	135.01
C4	22.54	14.75	7.79	22.04	9459	263.83	26.06	3.23	14.11	72.24	131.92
C5	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
C6	18.05	7.00	11.05	17.90	8160	195.73	21.03	nd	13.14	48.45	190.43
C7	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
C8	20.42	15.20	5.22	20.32	10084	214.58	28.98	3.02	18.21	180.65	175.14
C9	0.15	0.15		0.00	9971	216.33	118.67	3.09	17.89	100.07	249.66
C10	11.54	9.92	1.62	11.41	9943	211.76	30.44	3.25	18.39	112.33	261.54
C11	18.43	15.57	2.86	18.43	10875	213.32	32.01	3.55	20.68	82.43	309.99
C12	0.06	nd	0.06	nd	8656	169.83	25.49	2.76	17.67	27.70	261.72
D1	44.43	31.38	13.06	44.06	15323	382.01	45.62	6.70	18.40	3.15	nd
D2	47.31	32.76	14.55	46.61	12570	338.70	37.70	5.79	16.68	174.38	423.40
D3	40.56	31.23	9.33	40.18	11680	298.00	32.94	5.20	16.69	315.33	340.93
D4	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
D5	30.24	27.10	3.15	29.57	11441	300.17	36.72	4.94	17.86	190.80	101.49
D6	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
D7	54.69	43.34	11.35	54.51	12312	284.38	63.42	7.20	20.18	293.41	352.22
D8	25.61	22.06	3.55	25.13	9838	261.54	31.57	3.57	15.23	90.59	324.33
D9	31.04	15.46	15.58	30.75	11801	257.06	37.78	4.16	21.21	342.08	264.65
D10	8.88	8.79	0.09	8.76	10067	217.08	33.78	3.68	19.10	52.62	190.53
D11	14.50	8.68	5.81	14.45	8529	186.31	27.28	2.73	17.02	34.39	268.04
D12	4.93	4.04	0.89	4.89	8088	161.50	24.92	nd	16.18	16.18	309.51

Appendix 5

Appendix 5a) Summary of number of families (S), number of individuals (N), biomass g wet weight, Shannon diversity index log*e* (H') of small macroinfauna (>0.5 mm) per 0.01 m^2 at each Transect-Station (TS) sampled during two seasons in 1999 and 2000 in the Southern Gulf of Mexico. * Stations used for the ANOVA analysis, ns (not sampled stations).

	Rainy season November 1999				Northers season April 2000			
TS	**S**	**N**	**B**	**H'**	**S**	**N**	**B**	**H'**
*A1	15	43	0.069	2.45	12	67	0.132	1.85
A2	ns	ns	ns	ns	16	60	0.073	1.88
*A3	14	39	0.033	2.23	18	52	0.108	2.48
A4	14	34	0.034	2.21	ns	ns	ns	ns
*A5	9	13	0.034	2.10	9	17	0.018	1.96
*A6	1	1	0.001	0.00	5	9	0.009	1.52
*A7	7	9	0.023	1.89	3	4	0.007	1.04
*A8	4	5	0.024	1.33	16	22	0.032	2.63
*A9	1	1	0.001	0.00	10	14	0.025	2.14
A10	10	12	0.017	2.25	9	17	0.034	1.93
A11	9	13	0.023	2.10	20	27	0.024	2.89
*A12	8	11	0.011	2.02	8	12	0.011	1.98
B1	ns	ns	ns	ns	11	26	0.029	1.90
B2	12	31	0.039	2.20	28	170	0.577	2.24
B3	11	30	0.065	2.11	ns	ns	ns	ns
*B4	11	26	0.016	2.24	18	53	0.084	2.48
*B5	10	30	0.051	1.59	14	70	0.053	1.77
*B6	5	5	0.023	1.61	8	16	0.02	1.84
*B7	6	8	0.006	1.67	8	23	0.012	1.73
*B8	11	19	0.011	2.05	33	358	0.065	2.77
*B9	4	4	0.023	1.39	14	19	0.021	2.55
*B10	7	7	0.009	1.95	10	11	0.302	2.27
*B11	5	5	0.4	1.61	2	2	0.002	0.69
*B12	7	12	0.013	1.86	14	19	0.018	2.55
C1	8	8	0.032	2.08	13	17	0.085	2.45
*C2	3	5	0.003	0.95	2	2	0.003	0.69
*C3	2	4	0.002	0.56	4	6	0.008	1.24
*C4	2	2	0.002	0.69	5	5	0.006	1.61
C5	2	3	0.012	0.64	ns	ns	ns	ns
*C6	5	5	0.006	1.61	9	11	0.034	2.10
C7	3	7	0.023	1.08	ns	ns	ns	ns
*C8	5	5	0.007	1.61	8	10	0.038	2.03
C9	4	4	0.04	1.39	11	15	0.02	2.30
*C10	7	10	0.11	1.83	14	16	0.017	2.60
C11	4	4	0.004	1.39	6	6	0.006	1.79
C12	6	12	0.018	1.75	6	8	0.035	1.67

Appendix 5a (Continued)

	Rainy season November 1999				Northers season April 2000			
TS	S	N	B	H'	S	N	B	H'
*D1	7	10	0.008	1.83	14	25	0.036	2.39
*D2	6	6	0.007	1.79	13	25	0.052	2.48
*D3	4	4	0.006	1.39	7	11	0.011	1.85
*D4	5	5	0.005	1.61	ns	ns	ns	ns
*D5	11	17	0.024	2.34	10	20	0.017	2.09
D6	5	8	0.049	1.49	ns	ns	ns	ns
*D7	7	7	0.007	1.95	34	131	0.039	3.15
*D8	4	8	0.007	1.21	24	40	0.034	2.98
*D9	7	10	0.009	1.83	10	13	0.021	2.21
*D10	9	10	0.018	2.16	9	18	0.033	1.99
D11	17	31	0.041	2.69	22	38	0.039	2.93
*D12	17	27	0.06	2.67	14	19	0.14	2.51

Appendix 5b) Summary of number of families (S), number of individuals (N), biomass g wet weight, Shannon diversity index loge (H') of large macroinfauna (>2.0 mm) per 1 m^2 at each Transect-Station (TS) sampled during two seasons in 1999 and 2000 in the Southern Gulf of Mexico. * Stations used for the ANOVA analysis, ns (not sampled stations). NB Number of families and diversity are in 0.14 and 0.23/m^2 for November and April respectively.

	Rainy season November 1999				Northers season April 2000			
TS	S	N	B	H'	S	N	B	H'
*A1	11	109	8.9	2.30	28	860	9.0	2.14
A2	13	298	3.4	2.05	25	931	17.7	1.91
*A3	22	640	4.9	2.55	36	1106	6.4	2.93
A4	20	458	15.7	2.64	22	553	3.5	2.70
*A5	8	95	14.3	1.89	30	549	16.2	2.65
*A6	1	7	0.1	0.00	11	75	2.2	2.31
*A7	2	15	2.6	0.69	10	79	1.8	2.03
*A8	4	29	0.5	1.39	7	44	1.4	1.75
*A9	5	58	1.6	1.49	9	92	7.7	1.46
A10	2	15	0.2	0.69	ns	ns	ns	ns
A11	5	44	0.4	1.56	12	97	0.6	2.32
*A12	3	22	0.2	1.10	19	136	0.2	2.62
B1	12	153	87.0	2.31	29	672	5.9	2.53
B2	17	167	23.3	2.73	35	1102	21.1	2.57
B3	15	342	2.4	2.27	29	1927	15.3	2.18
*B4	12	138	22.3	2.33	21	808	11.3	2.34
*B5	8	211	4.9	1.46	7	75	1.3	1.72
*B6	2	22	0.8	0.64	8	70	0.7	1.65
*B7	3	22	1.4	1.10	15	101	1.3	2.43
*B8	5	44	0.2	1.56	11	97	1.3	2.14

Appendix 5b (Continued)

	Rainy season November 1999				Northers season April 2000			
TS	S	N	B	H'	S	N	B	H'
*B9	4	29	0.2	1.39	24	399	2.5	2.56
*B10	4	36	0.4	1.33	8	70	4.4	1.84
*B11	2	15	5.5	0.69	8	40	6.0	2.04
*B12	5	36	0.4	1.61	7	44	0.4	1.83
C1	5	51	1.3	1.55	12	119	2.5	2.27
*C2	7	58	5.0	1.91	9	75	2.1	2.04
*C3	2	29	1.6	0.56	6	35	0.5	1.73
*C4	3	29	1.9	1.04	8	83	0.5	1.73
C5	2	15	0.8	0.69	ns	ns	ns	ns
*C6	10	109	33.2	2.21	13	105	34.3	2.36
C7	5	36	15.1	1.61	ns	ns	ns	ns
*C8	4	36	4.4	1.33	9	75	2.7	1.87
C9	11	131	7.9	2.25	14	127	10.6	2.41
*C10	5	44	14.9	1.56	16	140	3.4	2.56
C11	8	95	1.5	1.74	11	110	3.1	2.12
C12	5	51	9.2	1.55	11	105	4.6	2.06
*D1	2	22	0.4	0.64	10	83	2.7	2.16
*D2	3	44	3.6	1.01	10	79	1.2	1.79
*D3	3	22	2.4	1.10	6	57	0.4	1.53
*D4	1	7	0.4	0.00	ns	ns	ns	ns
*D5	5	44	1.0	1.56	7	48	6.0	1.85
D6	4	29	0.5	1.39	ns	ns	ns	ns
*D7	0	0	0.0	0.00	9	57	1.1	2.10
*D8	4	36	0.5	1.33	12	101	3.1	2.28
*D9	8	80	10.0	2.02	7	44	1.0	1.83
*D10	9	65	21.5	2.20	12	83	12.5	2.30
D11	9	102	1.7	2.11	20	198	12.7	2.84
*D12	15	174	15.2	2.58	20	206	3.8	2.72

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