# Chapter 2

## 2. Species Assemblages

*"The loss of biodiversity is a human paradox and a crisis of technological culture"*

*(Kim and Weaver, 1994)*

This chapter compares species assemblages[1] present in hydraulically modified (inside FCDI schemes) and pristine (outside FCDI schemes) locations in Bangladesh based upon a re-examination of species abundance data recorded by FAP 17 using more robust statistical methodology. The data used in the analysis includes the PIRDP, and several other FCDI schemes in other regions of the country.

### 2.1 Introduction

Tropical fish communities[2] are noted for their high diversity (Lowe-McConnell, 1987). The floodplain river systems in Bangladesh contain more than 260 species of teleost fish within 145 genera and 55 families (Rahman, 1989). Fish communities are influenced by biotic and abiotic factors which are continually changing through space and time. These changes may occur gradually, for example in response to geomorphological change (land

1 A fish assemblage is "...all the fish species in a defined area..." Wootton, (1990) where a species is "... a group of similar individuals having a common origin and a continuos breeding system" (Lowe-McConnell, 1987).

2 The term 'community' is often used in the same way as 'assemblage', though the two may be distinct. The former comprise organisms that interact in some way in a given area or habitat, the latter include all the species present, irrespective of whether they interact or not (Wootton, 1990). The term 'assemblage' therefore offers a more general, widely applicable descriptor of groups of species.

form and levels), climatic change or more rapidly in response to anthropological effects such as pollution, exploitation and hydraulic engineering (Lowe-McConnell, 1987).

Changes to fish communities or assemblages have potentially important ecological, economic, nutritional, and arguably ethical and aesthetic implications (Spellerberg and Hardes, 1992; Robinson, 1993; Kim and Weaver, 1994). From an ecological perspective, these changes may affect the community dynamics and ecosystem functioning, leading to reductions in exploitable biomass (Wootton, 1990; Robinson, 1993; Kim and Weaver, 1994; Randall, 1994). Each successive loss of a species increases the probability of this occurring (Randall, 1994). Changes in species composition often result in the loss of large, high value species, lowering the overall unit value of the fishery. 'Replacement' species may compound this problem as they are often a small, low value 'opportunistic' type, characterised by low catchability and high cost of exploitation. Assuming prices remain unchanged, the net effect is a reduction in the economic rent of the fishery (Cunningham *et al*, 1985). Moreover, the nutritional value and processing costs per unit weight of fish may vary among assemblages comprising different sizes of fish particularly if processing efficiency varies with fish size (Regier *et al*, 1989). Perhaps of less apparent or immediate importance to developing nations is the concept that the value of biotic resources extends beyond its commercial or nutritional value; use and existence values are also important. Use value includes the aesthetic and recreation value of a resource (Randall, 1994). 'Existence value' is received by persons who feel pleasure from knowing that a resource is being maintained and protected. Likewise, 'bequest value' may be acquired from the satisfaction of knowing the resource will be available for future generations (Cunninghham *et al*, 1985). Perhaps more abstract are the ethical implications of such changes. These centre around the question of whether it is morally right or wrong to allow these changes to occur. The answer will depend largely on the prevailing religious and political beliefs (Spellerberg and Hardes, 1992).

Species inhabiting the floodplain-river systems have been categorised into two ecologically distinct groups based largely upon their behaviour in response to seasonal changes in the floodplain environment (Welcomme, 1985):

Whitefish

Species belonging to this category, are generally reophilic, inhabiting rivers and other fluvial bodies. The majority undertake seasonal spawning and/or feeding migrations either longitudinally (upstream) or laterally onto the floodplain, or a combination of both. Longitudinal migrations may be upstream or downstream, some are local covering only small distances, others, usually upstream, may be substantial. Upstream spawning locations offer a number of advantages, including higher dissolved oxygen concentrations and fewer predators. Furthermore, the duration of the downstream drift of developing fry may take several weeks allowing time for individuals to grow beyond a size which is particularly vulnerable to predation. Fry may move onto the floodplain either passively or actively or in the case of the anadromous *Hilsa ilsha*, be swept downstream to the sea. Adults of other species often return, usually before the eggs and young, to downstream floodplain habitats soon after spawning to take advantage of the rich feeding. Lateral migrations are active rather than passive and in an ordered sequence of species when returning to the main channel. Whitefish species are generally intolerant of the extreme conditions that exist in the floodplain habitat during the dry season (low oxygen and pH levels and high temperatures) and hence they must undertake lateral migrations to fluvial environments each year (Welcomme, 1985; Ward and Stanford, 1989).

Blackfish

Species belonging to this category are generally limnophilic, 'still-water fishes' (MRAG, 1994a). Because their migrations between wet and dry-season habitats are limited, they are normally confined to the floodplain habitat, dispersing within it during the flood to spawn and feed and inhabit residual water bodies and lagoons during the dry season. At most, their migrations are lateral to fringes of the main channel. Many species are adapted to surviving low oxygen concentrations, high temperatures and even desiccation (see Welcomme, 1985; Lowe-McConnell, 1987 for reviews).

This categorisation has been extended by Regier *et al* (1989) to include 'greyfish' species. 'Greyfish' species inhabit backwaters or the fringes of the main channel during the dry season and undertake lateral migrations to the floodplain for feeding and

spawning. However, unlike 'whitefish' species, they are capable of residing on the floodplain during the dry season if suitable conditions prevail.

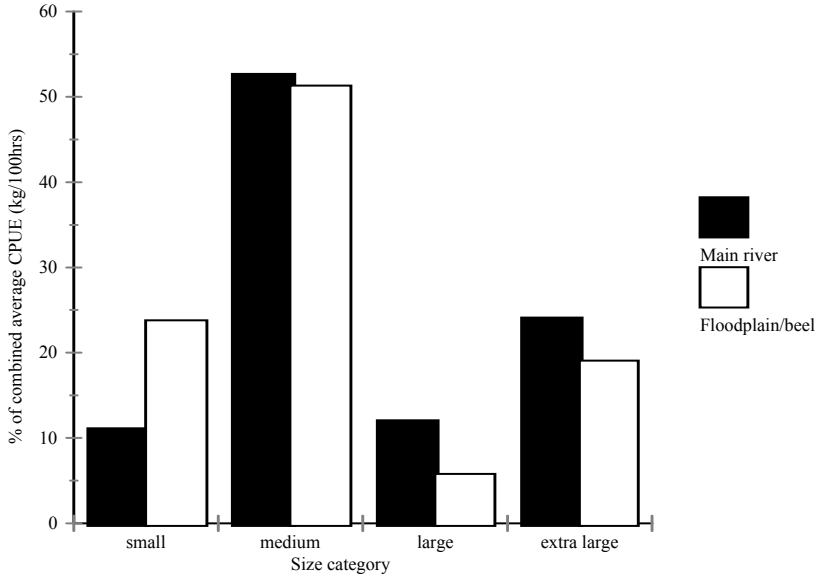
Species of fish are often also classified according to the main processes which control their populations, the intrinsic rate of population increase and the environmental carrying capacity (parameters *r* and *K* of the logistic population model). *'r*-selected' species are characterised by their small size, short lifespan, rapid growth, early maturity, high fecundity and high natural mortality rates (Pitcher and Hart, 1982). Their populations rely on the ability to colonise new habitats and increase rapidly to exploit unpredictable environments (eg inundated floodplain habitat). A consequence of these 'life history characteristics' is that their populations contain few age-groups and are intrinsically variable, 'tracking' the environmental variation. They can sustain high levels of exploitation, but are susceptible to sudden collapse (eg Peruvian anchovetta). Their small size makes them less mobile. Conversely, *K*-selected species are generally regarded as large, slow-growing, long-lived species, maturing later in life and usually less fecund. These species also tend to exhibit lower natural mortality rates. Their populations contain several age-classes and are therefore less susceptible to sudden collapse, but they cannot sustain heavy exploitation. They are less able to take advantage of favourable environmental conditions, but are better suited to surviving long periods of adverse conditions (Garrod and Knights, 1979; Pitcher and Hart, 1982; McDowall, 1994).

Size is seen as the most important trait of an individuals' life history and hence a good indicator of its position within the ' *r/K* spectrum'. As size decreases, metabolic rate per unit weight increases, leading to a decrease in longevity. The size of an organism has also been shown to be strongly positively correlated with its generation time and equally strongly negatively correlated with its intrinsic growth rate (Begon and Mortimer, 1986; McDowall, 1994).

It is postulated that because it is largely the environment which 'selects' for species (Begon and Mortimer, 1986) those which primarily reside, or can choose to reside, on the floodplain ('blackfish' and 'greyfish' respectively) all year round are likely

predominantly to comprise *r*-selected species, but will also include some *K*-selected species which have developed adaptations to surviving on the floodplain. An example of the latter might include *Channa straitus*, a relatively large, slow growing, low fecundity piscivorous predator which has a modified supra-branchial chambers adapted for air breathing (see Welcomme, 1985 for further details*)*. Conversely, given the relative 'stability' of the riverine environment, 'whitefish' species are likely to comprise mostly *K*-selected species, but will also include some *r*-selected species, mostly clupeids.

Arguably, this postulate would be supported to some degree if riverine habitats contained more large species than small, and if floodplains contained relatively more small species than large. Figure 2.1 below shows the average abundance of species belonging to four size categories; small (<30cm), medium (30-60cm), large (60-90cm) and extra large (>90cm) caught from main river and floodplain habitat in pristine locations in




Bangladesh during 1993. Average abundance (kg/100 hours of fishing with a small mesh seine) is expressed as a percentage of the combined catch per unit effort (CPUE) which was averaged across the species within each size category.

Figure 2.1 Comparison of the percentage of combined average abundance (kg/100 hours of fishing) of species belonging to small, medium, large and extra large fish caught in main river and floodplain habitat in Bangladesh during 1993 using seine net gear. (Data source: FAP 17 Database).

Small species are more abundant on the floodplain compared with the main river habitat and large and extra large species are more abundant in the main river compared to the floodplain habitat (Figure 2.1) supporting the postulate. The presence of large and extra large species on the floodplain is likely to reflect the migratory behaviour of these individuals as large size is likely to be an asset for fish that migrate (McDowall, 1994). Welcomme (1979: p86-87) hints at the presence of a difference in the size structure of species inhabiting these two main biotopes: "...there tends to be a high proportion of fish of very small adult size (less than 10cm) on floodplains..." and "...most river systems have a few species of truly gigantic size".

As we shall see later, this apparent spatial difference in the abundance of *r* and *K*-selected species has important implications for interpreting differences in species assemblages.

Previous studies which have investigated the impacts of levees and polders (FCDI schemes in Bangladesh) were summarised in Table 1.1 of the previous chapter. These

studies indicate that their main impact is to interrupt migratory pathways and the passive drift of larvae and juveniles onto the floodplains. The overall effect is to eliminate lateral migrants and reduce recruitment or cause complete recruitment failure of species relying on the passive drift of larvae/juveniles onto the floodplain (Butcher, 1967; Starret, 1972; Sparks and Starret, 1975; Balcalbasa and Popta, 1978; Welcomme, 1979, 1985; Fremling *et al*, 1989; FAP 17, 1994). FCDI schemes also have the potential to affect species assemblages indirectly, largely as the result of higher human population densities which are likely to be attracted to the relative security and stability of the modified floodplain environment offered by embankments or levees. These higher population densities are likely to have a greater polluting potential resulting from more intensive use of pesticides and fertilizers required for HYV's of crops, and from potentially greater concentrations of domestic and urban waste (Welcomme, 1979, 1985 Table 8.4; Regier *et al*, 1989; Natarajan, 1989; Sklar and Dulu, 1994).

These higher human population densities are also likely to lead to a much higher level of fishing intensity (fishing effort per unit area) which in turn can bring about changes to fish assemblages (see below).

Changes to fish communities or assemblages in response to increasing fishing intensity is largely predictable and often termed 'ecosystem overfishing' or the 'fishing-up process' (Regier and Loftus, 1972). The fishing-up process has been widely observed in a number of freshwater ecosystems including the Amazon, Orinoco, Oueme, Mekong river and several of the Great African Lakes (Welcomme, 1985). Commonly, as exploitation increases, there is a progressive disappearance of larger (*K*-selected) species, which are usually highly mobile (migratory) or predatory (piscivorous) and targeted as highly valuable food fish (Regier, 1977; Regier *et al*, 1989). These species tend to be particularly vulnerable to fishing gear. Predators are generally aggressive with high catchability to gear such as baited hooks and lines. Large aggregations of migratory species become highly vulnerable to relatively efficient barrier or interceptory type traps and nets as knowledge of their behaviour, location of their spawning sites and migration routes become progressively more understood. Although these species are well adapted to moderate fishing intensity, they are readily overfished at high levels of exploitation.

Elimination of the large predatory species frequently results in the community becoming dominated by small, short-lived, opportunistic (*r*-selected) species including crustacea and which contain few piscivorous or large migratory or benthic (*K*-selected) species. Catches become progressively dominated by smaller, lower value species which tend to exhibit large interannual variation in abundance linked to inter-annual variations in flood strength. However, because these small species often occupy a lower trophic level, overall production may not be diminished, rather the rate of biological production is expected to increase, which coupled with a reduction in the population biomass leads to a higher production/biomass ratio (P/B) (Regier and Loftus, 1972; Regier and Henderson, 1973; Regier, 1977; Garrod and Knights, 1979; Tuner, 1981; Welcomme, 1985; LoweMcConnell, 1987; Novoa, 1989; Regier *et al*, 1989; Welcomme *et al*, 1989). Based upon these ideas, heavily exploited floodplain communities would be expected to become dominated by small *r*-selected 'blackfish and 'greyfish' species.

Because *K*-selected 'whitefish' species are often migratory and predatory, a communitys' response to the effects of FCDI schemes may be very similar to one which has suffered very high exploitation levels. A further complication arises because other forms of environmental stress other than exploitation by man (eg pollution) can bring about similar responses (Welcomme, 1985). Therefore it may be very difficult to elicit and separate the causal mechanisms of an observed community or assemblages response to hydraulic engineering (Regier *et al*, 1989; Welcomme *et al,* 1989).

Evidence also suggests that species assemblages are able to respond to natural, particularly climatic, variations in the environment. For example in the River Niger, two homologous assemblages appear to exist, one of which is adapted to poor flood and the other to high flood conditions. This flexibility also extends to the species level, typified by the ability of species such as common carp, to change their migratory behaviour in response to the prevailing hydrological conditions (Welcomme, pers.comms.).

## 2.2 Methods for studying multi species distribution patterns

The bewildering array of methods and techniques for analysing ecological communities may be broadly categorised into three distinct groups:

(1) Univariate methods

These condense the species counts for a sample (site) into a single coefficient, typically a diversity index. A number of indices, often in combination, are commonly used in fisheries research including the Simpson's Diversity Index (*D*), Shannon-Wiener Diversity Index ($H^{/}$), and species richness (*S*) (Wootton, 1990). For impact studies, discrimination between sites is often demonstrated with one-way analysis of variance using a number of replicates recorded for each site, condition or time period, followed by multiple comparison tests (eg Tukey, 1953) for individual pairs of sites or conditions. For species richness, values may first have to be logged in order to meet normality and constant variance conditions. Linking patterns of diversity with the environment is usually performed using simple (or multiple) regression techniques (Clarke and Warwick, 1994). A particular weakness of diversity indices is that in themselves they contain no biological information (Wootton, 1990) and so two samples or sites may have

the same diversity, but without possessing a single species in common (Clarke and Warwick, 1994). Therefore, although the environmental impact may be described in terms of differences in diversity, the causal mechanisms will not be revealed.

(2) Graphical/Distributional methods

Graphical/distributional representations extract information on patterns of relative species abundance or biomass without condensing the information into a single summary statistic such as a diversity index. These methods are used in pollution studies, specifically as a means of determining levels of environmental 'stress'. They are not regarded as applicable to this research and thus are not given further consideration here. Further details of these methods are described in Sanders (1968), Gray and Pearson (1982), Warwick (1986) and Clarke and Warwick (1994).

(3) Multivariate methods

Multivariate methods are those which deal with large numbers of measurements recorded in one or more samples simultaneously. Instead of focussing on the analysis of mean and variance, they direct attention to the analysis of correlations or (dis)similarities among the data (Dillon and Goldstein, 1984). They are "... descriptive techniques for exploring pattern in data sets and providing succinct summaries and displays" (Digby and Kempton, 1987). Since community data are inherently multivariate, Clarke and Warwick (1994) argue in favour of these methods "...in order to elicit the important biological structure and its relation to the environment". This approach is often termed 'pattern analysis'. Two major categories of multivariate approaches for analysing ecological communities exist: ordination and classification methods (Figure 2.2).

Ordination methods

Ordination methods attempt to construct 'maps' of samples, usually in a low number of dimensions (two or three), such that their placement reflects the similarity of their biological communities. Points in close proximity to each other have very similar communities whilst samples that are far apart share few common species or have the same species but at very different levels of abundance or biomass (Clarke and Warwick, 1994).

Two categories of ordination may be defined (Figure 2.2). The first are referred to as indirect gradient analysis techniques. These aim to produce sample maps to provide insight into the underlying structure of the data by simplifying the complexities through data reduction (Dillon and Goldstein, 1984), thereby aiding the generation of hypotheses regarding the relationships between species compositions and environmental factors (Digby and Kempton, 1987). In essence these techniques allow the data to "...tell its own story.."(Clarke, 1993). In contrast, direct gradient analysis (ordination) techniques represent an intermediate between regression analysis and ordination. These are the 'canonical ordination techniques' which deal simultaneously with species and environmental data (Jongman *et al*, 1987). However, these methods have been largely criticised for embedding *a priori* assumptions about species-environment responses at an early stage of the analysis (Jongman *et al* 1987; Clarke, 1993). Typically, the response is assumed to be unimodal, though in reality the form of the response may be linear, unimodal, monotonic or multimodal or combinations of these (Clarke, 1993). However, this criticism is not unique to direct gradient methods, but also extends to some of the indirect methods. Direct gradient methods are further complicated by the fact that invariably there are many environmental variables which can be measured and it is often not known which variables the species react to (Jongman *et al*, 1987).

The major categories of ordination methods falling into the direct and indirect gradient analysis techniques are briefly described below.

(i) Indirect gradient analysis techniques

Principal Components Analysis

Principle components analysis was the first ordination method to be devised. The method assumes a linear response model in which the abundance of any species either increases or decreases with the value of the latent environmental variables (Jongman *et al*, 1987). It aims to produce an ordination of the samples which emphasises the major patterns of variation in species composition (Digby and Kempton, 1987). This is achieved by transforming the data array into a set of linear combinations that account for

most of the variance in the original data set (Dillon and Goldstein, 1984). Implicitly, dissimilarities between samples are defined in terms of their Euclidean distance (the natural distance in space) which are converted onto the ordination by projection. The success of the (two-dimensional) ordination is measured as the percentage of total variation explained by the first two principal components (Clarke and Warwick, 1994). Although PCA is conceptually straightforward, it does have a number of weaknesses. Firstly, Euclidean distance is not a particularly suitable measure of dissimilarity between samples because it takes account of joint absences. A measure which "...takes account of joint absences has the effect of saying estuarine and abyssal samples are similar because both lack outer-shelf species" (Field *et al*, 1982).

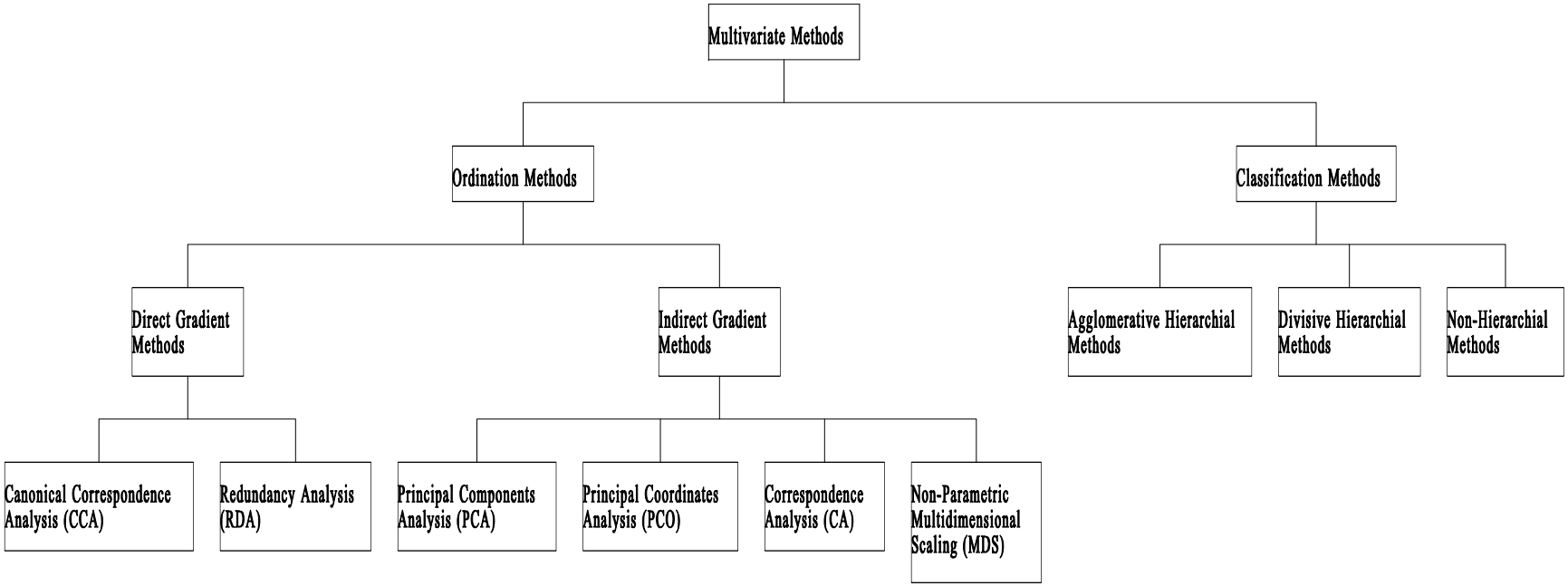



Figure 2.2 Classification of multivariate methods for analysing ecological community data.

Biological survey data are often characterised by absences of many species in the majority of samples so that data arrays are often dominated by zeros (Field *et al*, 1982). Secondly, PCA requires the exclusion of less common species for the algorithm to work, so that the number of species retained is comparable to the number of samples. This often necessitates arbitrary decisions about which species to exclude. Thirdly, as stated above, it makes assumptions about the form of the species-environment response model. Finally, its distance-preserving properties are regarded as poor (Clarke and Warwick, 1994).

Principal Coordinates Analysis

Principal Coordinates Analysis (PCO) or classical scaling is an extension of PCA. It aims to addresses the weakness of its Euclidean dissimilarity measure by allowing a wider definition of dissimilarity measures. However, as with PCA, its distance preserving properties are poor and it assumes a linear response model (Clarke and Warwick, 1994).

Correspondence Analysis (CA)

Correspondence analysis (CA) is a technique that constructs a theoretical variable that best explains the species data by iteratively selecting values for sites that maximise the dispersion of species scores (an estimate of the optimum value of the theoretical variable for the species). This theoretical variable is termed the first ordination axis of CA; its values are the site scores on the first CA axis. A second and further axes may be constructed that successively improve the dispersion of species scores with the constraint of being uncorrelated with previous CA axes (Jongman *et al*, 1987).

A particular weakness of this ordination method is its sensitivity to the 'horseshoe effect'(Greig-Smith, 1983; Kershaw and Looney, 1985; Digby and Kempton, 1987). This is often observed when samples have been taken from diverse habitats along a single environmental gradient when instead of a linear sequence of sites, the ordination shows an arch or horseshoe shape. In this case, the ordination therefore fails to represent the true underlying (dis)similarity between sites. Detrended correspondence analysis (DECORANA) was proposed by Hill and Gauch (1980) as a modified version of this

technique which aims to overcome these faults. The method consists of a trend removal method and optional rescaling of axis to remove compression points at either end (Digby and Kempton, 1987; Jongman *et al*, 1987). However, this process has been widely criticised for being arbitrary and "overzealous" in its manipulation of the data (Digby and Kempton, 1987; Clarke, 1993; Clarke and Warwick, 1994). Both CA and DCA assume unimodal species-environment response models.

Non-metric multidimensional scaling (MDS)

Non-metric Multidimensional scaling (MDS) was developed by Shepard (1962) and Kruskal (1964) for use in social sciences where measurement scales are often arbitrary. Since its development it has been extensively used in a large number of published ecological studies (Clarke, 1993). The method constructs an ordination where the relative distances between samples or sites are based upon their rank (dis)similarity calculated from a matrix of similarity or dissimilarity coefficients. The coefficient is usually a simple algebraic measure of how close the abundance levels are for each species. The MDS algorithm employs an iterative procedure to construct the ordination, successively moving the positions of the points until they satisfy the dissimilarity relations between the samples. The success of the ordination is measured in terms of 'stress' (Clarke and Warwick, 1994). The ordination is then interpreted in terms of relative similarities, for example, "sample A is more similar to sample B than it is to sample C" (Clarke, 1993).

A particular strength of this technique is its lack of assumptions regarding the form of the species-environment response. Its distance preserving properties (based upon the rank order of dissimilarities) are also superior to those based upon actual numerical values of the dissimilarities such as PCA and CA. Rohlf (1972) conducted an empirical comparison of non-metric MDS, PCA and PCO applied to numerical taxonomy and found that MDS gave the best results as measured by the correlation between the distances in the ordination and the original dissimilarity distances. The method also provides flexibility in the choice of similarity coefficients that can be utilized which can be chosen to ignore joint absences, to place emphasis on common or rare species or compare percentage species composition. Furthermore, MDS is conceptually simple and

therefore may be readily applied with understanding and the results easily communicated (Clarke and Warwick, 1994). The weakness of this approach is that the iterative procedure cannot guarantee to reach the global optimum (Digby and Kempton, 1987; Clarke and Warwick, 1994). This makes it necessary to repeat the analysis several times from different starting configurations to ensure the global minimum of the stress function has been reached (Clarke and Warwick, 1994).

(ii) Direct gradient analysis methods (Canonical ordination techniques)

Canonical ordination techniques aim to detect patterns of variation in community data that can be best explained by observed environmental variables. This is achieved using an ordination that maps the pattern in variation in species compositions between sites but also the main relations between the species and environmental variables. Two methods are commonly used, the first, Canonical Correspondence analysis (CCA), is an extension of correspondence analysis. The second, Redundancy analysis (RA), is the canonical form of PCA (Jongman *et al*, 1987).

Direct gradient methods are impossible to perform without explicit environmental data (Jongman *et al*, 1987). The species data analysed in this chapter have no corresponding environmental data with which they may be interpreted and therefore no further examination of these methods is given here. A good description of these methods is given in Jongman *et al* (1987).

Classification Methods

These are techniques for classifying sites, species or variables into natural groupings by identifying inherent structure in the data (Jongman *et al*, 1987). The methods often provide a useful and objective preliminary classification system (Digby and Kempton, 1987). Three major categories of classification methods can be identified: agglomerative, divisive hierarchial and non-hierarchial methods. Agglomerative hierarchial methods, commonly termed 'cluster analysis', are the most commonly employed classification methods in community ecology (Clarke and Warwick, 1994). The methods employ a similarity matrix calculated for the samples or sites and

successively fuse them into groups or clusters starting with the two most similar samples (Gauch, 1982; Digby and Kempton, 1987). Divisive hierarchial methods execute the converse sequence, starting with a single cluster and successively dividing it into smaller groups. The results of hierarchial clustering are usually presented in the form of a dendrogram (tree diagram) which shows the hierarchial structure and similarity level between sites and groups of sites (Jongman *et al*, 1987). Dendrograms do, however, have a number of disadvantages associated with them which have been described by Field *et al* (1982): (i) they only show inter-group relationships, (ii) they have a tendency to overemphasise discontinuities and may force a graded series into discrete classes, and (iii) the sequence of samples in the dendrogram is arbitrary and two adjacent samples are not necessarily the most similar which can make their interpretation difficult.

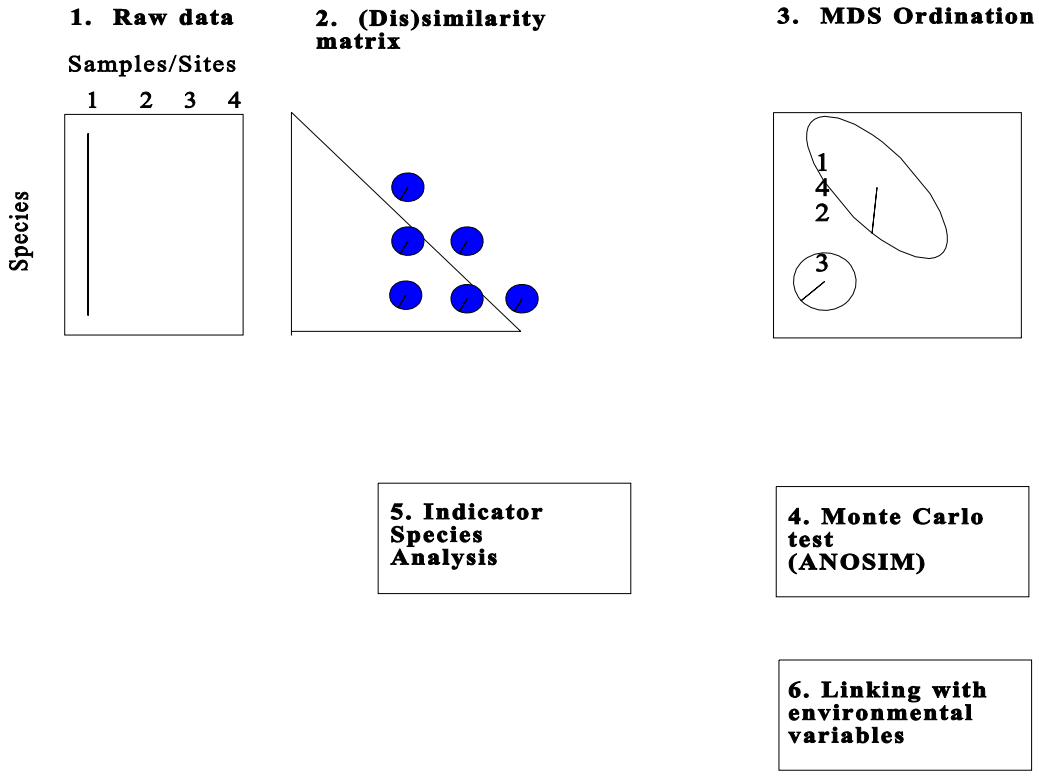
Non-hierarchial classification methods are conceptually the simplest of all multivariate techniques. These methods assign each sample to a cluster positioning similar samples together (Gauch, 1982). This is usually achieved by selecting sites or samples to act as initial foci for clusters and then assigning other sites to the clusters. Further details of the methodology and available software are described by Gauch (1982) and Jongman *et al* (1987). Unlike hierarchial classification, these methods are unable to elicit the relationships between clusters, but may provide an initial first step in clustering of very large data sets (Gauch, 1982).

## 2.3 Materials and methods

From the plethora of multivariate techniques outlined above, non-parametric multi-dimensional scaling was selected for the analysis in this chapter because of (i) its lack of

assumptions regrading the form of the species-environment response and (ii) its flexibility in terms of definition and conversion of dissimilarity to distance and preservation of these relationships in ordination space. The multivariate approach adopted in this chapter (Figure 2.3) is based upon a strategy proposed by Clarke and Warwick (1994).

Figure 2.3 Summary of the stages and pathways in the multivariate analyses used in this section.




Raw data

The analysis presented in this chapter is based upon species catch and effort data recorded by FAP17 at 104 different sampling sites in Bangladesh during 1993. These sites are located in the north west (NW), north central (NC), north east (NE) and south

west (SW) regions of the country. The sites represent the full range of aquatic habitat categories found in the country and are subject to varying degrees of hydrological control. Site habitat have four categories;

| | | | |
|---|---|---|---|
| (i) | Main rivers (MR) | : | Jamuna and Padma |
| (ii) | Secondary rivers (SR): | | small rivers |
| (iii) | Canals/khals (C) | : | channels linking rivers to floodplains/beels |
| (iv) | Floodplain/Beel (FB) | : | seasonally flooded land/depressions on floodplain |

Sites located outside FCDI schemes, and therefore not subjected to any form of hydrological control, were classified as 'pristine'. All sites located within FCDI schemes were classified as 'modified' though the degree of hydrological control within them may vary because some are structurally incomplete or have breached or submersible embankments. The degree of hydrological control within each scheme was classified as:

| | | |
|---|---|---|
| None | - | The site is not located within a FCDI scheme or the construction of the FCDI is incomplete. |
| Partial | - | The FCDI scheme has submersible or breached embankments. |
| Full | - | The embankments of the FCDI scheme are intact and flood levels within the scheme are controlled by sluice gates and pumps. |

Sites are identified by an alphanumeric code, for example, NW11, SW26. The alphabetical symbols donate the region of the country, and the number identifies a particular sampling site within that region. Full details of each site are given in Table 2.1.

Table 2.1 Descriptions of FAP 17 sampling sites including degree of hydrological regulation. CPP-Compartmentalization Pilot Project, MIP-Manu Irrigation Project, SHP-Shanghair Haor Project, PIRDP- Pabna Irrigation and Rural Development Project, BRE-Brahmaputra Right Embankment, PB- Polder B, CFP- Chatla-Fukurhati Project. P - Pristine habitat, M- Modified habitat.

| Site code | Site Description | Habitat code | In/ out | FCD/I scheme | Degree of regulation | Comments |
|---|---|---|---|---|---|---|
| NC01 | Jamuna River | MR | P | | None | Pristine habitat |
| NC02 | Pungli River | SR | P | | None | Pristine habitat |
| NC03 | Gala & Borobasalia Khals | C | P | | None | Pristine habitat |
| NC04 | Gazaria Floodplain | FB | P | | None | Pristine habitat |
| NC05 | Tepi Beel | FB | P | | None | Pristine habitat |
| NC06 | Northern Dhaleswari River | SR | P | | None | Pristine habitat |
| NC07 | Anahula Khal | C | P | | None | Pristine habitat |
| NC08 | Anahula Floodplain | FB | P | | None | Pristine habitat |
| NC09 | Anahula Beel | FB | P | | None | Pristine habitat |
| NC10 | Indrabelta and Santosh Khals | C | M | CPP | None | Construction incomplete |
| NC11 | Beltaraksit Floodplain | FB | M | CPP | None | Construction incomplete |
| NC12 | Lohanjang River | SR | P | | None | Pristine habitat |
| NC13 | Deojang and Atia Khals | C | M | CPP | None | Construction incomplete |
| NC14 | Atai Floodplain | FB | M | CPP | None | Construction incomplete |
| NC15 | Atai Beel | FB | M | CPP | None | Construction incomplete |
| NC16 | Dhaleswari River | SR | P | | None | Pristine habitat |
| NC17 | Zia Khal | C | P | | None | Pristine habitat |
| NC18 | Mailjani Floodplain | FB | P | | None | Pristine habitat |
| NC19 | Mailjani Beel | FB | P | | None | Pristine habitat |
| NC20 | Jamuna River | MR | P | | None | Pristine habitat |
| NC21 | Gazikhali River | SR | P | | None | Pristine habitat |
| NC22 | Chandrakhali Khal | C | P | | None | Pristine habitat |
| NC23 | Hazipur Floodplain | FB | P | | None | Pristine habitat |
| NC24 | Hazipur Beel | FB | P | | None | Pristine habitat |
| NC25 | Dhaleswari River | SR | P | | None | Pristine habitat |
| NC26 | Mailagi Khals | C | P | | None | Pristine habitat |
| NC27 | Char Ghior Floodplain | FB | P | | None | Pristine habitat |
| NC28 | Char Ghior Beel | FB | P | | None | Pristine habitat |
| NC29 | Ichamati River | SR | P | | None | Pristine habitat |
| NC30 | Sakini Khal | C | P | | None | Pristine habitat |
| NC31 | Gala Floodplain | FB | P | | None | Pristine habitat |
| NC32 | Jamuna River | MR | P | | None | Pristine habitat |
| NC33 | Jamuna river | MR | P | | None | Pristine habitat |
| | | | | | | |
| NE01 | Khorodari Khal | C | M | MIP | Partial | Embankments breached |
| NE02 | Islampur Floodplain | FB | M | MIP | Partial | Embankments breached |

| Site code | Site Description | Habitat code | In/ out | FCD/I scheme | Degree of regulation | Comments |
|---|---|---|---|---|---|---|
| NE03 | Akali Gang | C | M | MIP | Partial | Embankments breached |
| NE04 | Patasinga Beel | FB | M | MIP | Partial | Embankments breached |
| NE05 | Baraimabad Floodplain | FB | M | MIP | Partial | Embankments breached |
| NE06 | Kushiyara River | SR | P | | None | Pristine habitat |
| NE07 | Juri River | SR | P | | None | Pristine habitat |
| NE08 | Tekuni Floodplain | FB | P | | None | Pristine habitat |
| NE09 | Tekuni Beel | FB | P | | None | Pristine habitat |
| NE10 | Gobindapur Floodplain | FB | P | | None | Pristine habitat |
| NE11 | Old Surma River | SR | P | | None | Pristine habitat |
| NE12 | Mouti Beel | FB | M | SHP | Partial | Submersible embankments |
| NE13 | Karchabrar Beel | FB | M | SHP | Partial | Submersible embankments |
| NE14 | Asumura Floodplain | FB | M | SHP | Partial | Submersible embankments |
| NE15 | Lumardai Khal | C | M | SHP | Partial | Submersible embankments |
| NE16 | Surma River | SR | P | | None | Pristine habitat |
| NE17 | Dapha Floodplain | FB | P | | None | Pristine habitat |
| NE18 | Dapha Beel | FB | P | | None | Pristine habitat |
| NE19 | Chatal Beel | FB | P | | None | Pristine habitat |
| NE20 | Mahasingh River | SR | P | | None | Pristine habitat |
| | | | | | | |
| NW01 | Jamuna River | MR | P | | None | Pristine habitat |
| NW02 | Jamuna & Hursagar Rivers | MR | P | | None | Pristine habitat |
| NW03 | Badai River | SR | M&P | PIRDP | Full | |
| NW04 | Gandahasti Floodplain | FB | M | PIRDP | Full | |
| NW05 | Gazna Beel | FB | M | PIRDP | Full | |
| NW06 | Ichamati River | SR | M | PIRDP | Full | |
| NW07 | Kageswari River | SR | M | PIRDP | Full | |
| NW08 | Roadside canals | C | M | PIRDP | Full | |
| NW09 | Gangbhanga Floodplain | FB | M | PIRDP | Full | |
| NW10 | Gangbhanga Beel | FB | M | PIRDP | Full | |
| NW11 | Chiknai River | SR | M | PIRDP | Full | |
| NW12 | Shwargram Floodplain | FB | M | PIRDP | Full | |
| NW13 | Shwargram Beel | FB | M | PIRDP | Full | |
| NW14 | Baral River | SR | IM | PIRDP | Full | |
| NW15 | Karatoya River | SR | P | | None | Pristine habitat |
| NW16 | Borrow Pit Canals | C | P | | None | Pristine habitat |
| NW17 | Baghabari Floodplain | FB | P | | None | Pristine habitat |
| NW18 | Sunnai Beel | FB | P | | None | Pristine habitat |

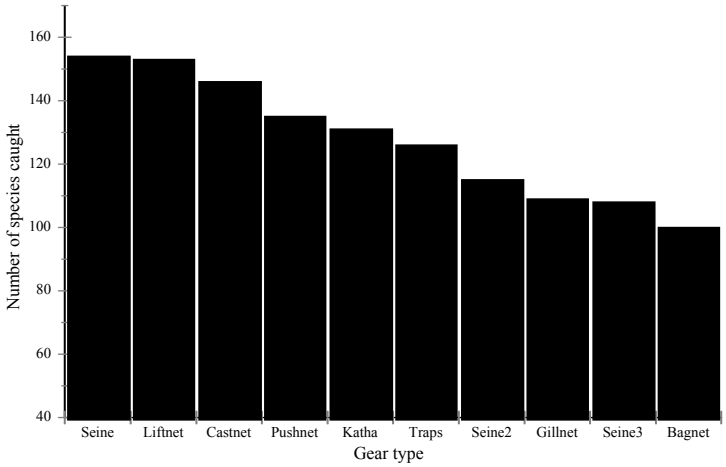
| Site code | Site Description | Habitat code | In/ out | FCD/I scheme | Degree of regulation | Comments |
|---|---|---|---|---|---|---|
| NW19 | Old Hurasagar River | SR | M | BRE | Full | |
| NW20 | Nandina Khal | C | M | BRE | Full | |
| NW21 | Nandina Beel | FB | M | BRE | Full | |
| NW22 | Pabna Beel | FB | M | PIRDP | Full | |
| NW23 | Someshpur Beel | FB | M | PIRDP | Full | |
| NW24 | Padma River | MR | P | | None | Pristine habitat |
| NW25 | Baral River | SR | M | PIRDP | Full | |
| NW26 | Chargat Beel | FB | M | PIRDP | Full | |
| NW27 | Atrai River | SR | P | | None | Pristine habitat |
| NW28 | Haribhanga Beel | FB | M | PB | Full | |
| NW29 | Chalan Khals | C | P | | None | Pristine habitat |
| NW30 | Chalan Beel | FB | P | | None | Pristine habitat |
| | | | | | | |
| SW01 | Padma River | MR | P | | None | Pristine habitat |
| SW02 | Arial Khan River | SR | P | | None | Pristine habitat |
| SW03 | Bhubaneswar River | SR | P | | None | Pristine habitat |
| SW04 | Bogail Khal | C | M | CFP | Partial | Breached embankments |
| SW05 | Kumardanga Floodplain | FB | M | CFP | Partial | Breached embankments |
| SW06 | Chatla Beel | FB | M | CFP | Partial | Breached embankments |
| SW07 | Kumar River | SR | P | | None | Pristine habitat |
| SW08 | Rajandi Khal | C | P | | None | Pristine habitat |
| SW09 | Mohipauls Floodplain | FB | P | | None | Pristine habitat |
| SW10 | Andolir Beel | FB | P | | None | Pristine habitat |
| SW11 | Amgramer Khal | C | P | | None | Pristine habitat |
| SW12 | Kalabari Khal | C | P | | None | Pristine habitat |
| SW13 | Josler Floodplain | FB | P | | None | Pristine habitat |
| SW14 | Joisler Beel | FB | P | | None | Pristine habitat |
| SW15 | Moisler Floodplain | FB | P | | None | Pristine habitat |
| SW16 | Moizler Beel | FB | P | | None | Pristine habitat |
| SW17 | Satla-Bagda Khal | C | P | | None | Pristine habitat |
| SW18 | Chitrapara Floodplain | FB | M | SBP | Full | |
| SW19 | Chitrapara Beel | FB | M | SBP | Full | |
| SW20 | Ambola Khal | C | M | SBP | Full | |
| SW21 | Ambola Floodplain and Beel | FB | M | SBP | Full | |
| SW22 | Satla-Bagda Floodplain | FB | M | SBP | Full | |

Data format

The analysis was based upon annual catch per unit effort (CPUE) data recorded for each species and site for a single gear type. Because no estimates of standardised effort were available for any one gear type used at all the sites, the CPUE data used in the analysis are uncorrected for any effects that season and habitat type might have upon catchability. However, CPUE is a more meaningful index of abundance than the percentage contribution to the total catch and using data for only a single gear type also overcomes the problems associated with the 'gear' and 'effort mix' described in Section 1.4. By using the data in this format, the major criticisms of the approach adopted by FAP17 (1995b) were addressed. The CPUE values were calculated from the total annual catch (kg) of each species and the total effort (hours fished) recorded for the gear at each site and expressed in terms of catch per 100hrs of fishing effort as catch rates were generally very low.

Gear selection

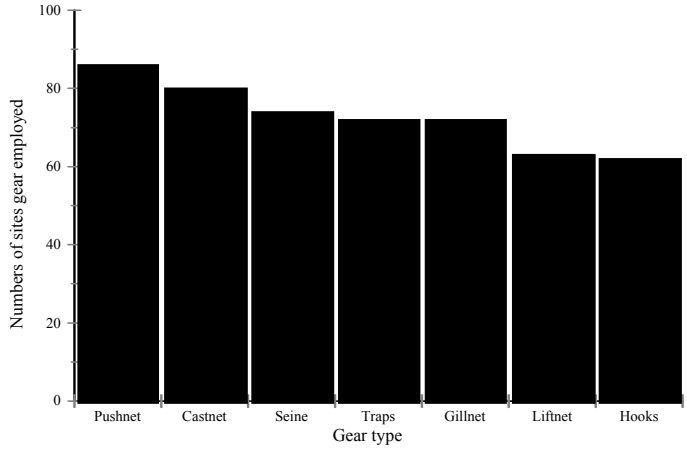
Two criteria, species selectivity and site coverage, were used to select the most appropriate gear for this analysis from the seventy one different types recorded at the sites during 1993. Selectivity was measured as the number of species caught by the gear. The greater the number of species caught, the lower the selectivity and *vice versa.* Site coverage was measured as the number of sites where the gear was used. The most appropriate gear was deemed to be unselective, or have the lowest selectivity, and was used at all or most of the sampling sites. Figure 2.4a compares the selectivity of the different gears which caught more than 100 species. The small mesh seine (gear code '45') caught more species (154) than any other gear type and was therefore the least selective. These 154 species accounted for 99.9% of the combined annual catch from all gear types during 1993. Figure 2.4(b) shows the numbers of sites where individual gears catching more than 100kg were recorded during 1993. Gear-site combinations with catches less than this arbitrary figure were not included because it was believed that small catches would not contain a representative sample of the species assemblage.


160
140
120
100
80
60
40
Number of species caught
Seine
Liftnet
Castnet
Pushnet
Katha
Traps
Seine2
Gillnet
Seine3
Bagnet
Gear type

(a)

(b)

Figure 2.4 (a) Number of individual species caught by the different gear types employed at the sampling sites during 1993. Only gears that caught more than 100 species are




shown. The gear labelled 'Seine' is 'gear 45'. Seine2 and 3 are other types of seine net. (b) Numbers of sites where individual gears catching more than 100 kg were recorded during 1993. Only gears recorded at more than 50 sites are shown. Data source: FAP 17 Database.

The pushnet was recorded at more sites (86) than any other gear. The castnet ranked second with 80 sites and seine net (gear 45) third, with 74 sites. The fact that no single gear was used at all 104 sites, serves to reinforce the fact that the 'gear mix' is unlikely to be the same among sites. Given the rationale of this chapter, selectivity was considered a

more important attribute than coverage and therefore it was concluded that the seine net (gear 45) was the most appropriate gear for this analysis.

Data matrix

The CPUE data for gear 45 are presented in the form of a typical rectangular species-by-site matrix in Table A2.1. Only sites where catches by gear 45 exceed 100 kg are included. The matrix comprises 154 rows, corresponding to the number of species in the sample and 74 columns corresponding to the number of sites. The abundance of the *i*th species at the *j*th site is donated by $y_{ij}$.

(Dis)similarity matrix

Multivariate methods are based upon the concept of similarity measured between pairs of samples. Similarity between samples is measured by a similarity coefficient (*S*) which is usually defined to take values in the range 0-100% where:

S = 100% if two samples have identical species assemblages;
S = 0 if two samples have totally dissimilar species assemblages.

A number of similarity measures are widely used in ecology. The attributes of the most common have been described by Field *et al* (1982), Digby and Kempton (1987) and Clarke and Warwick (1994). Clarke (1993) and Clarke and Warwick (1994) argue in favour of the Bray-Curtis coefficient (Bray and Curtis (1957)) based upon the findings of Faith *et al* (1987), because it is invariant to scale change, and is not affected by joint absences. All the multivariate analyses presented in this chapter employ this coefficient. The Bray-Curtis similarity ($S_{jk}$) between the *j*th and *k*th samples in the data matrix, is given by:

$$S_{jk} = 100\left(1 - \frac{\sum_{i=1}^{p} | y_{ij} - y_{ik} |}{\sum_{i=1}^{p} ( y_{ij} + y_{ik} )}\right) \qquad (1)$$

where

$y_{ij}$ = abundance or biomass of the *i*th species in the *j*th sample, and
$y_{ik}$ = abundance or biomass of the *i*th species in the *k*th sample.

Similarities calculated between every pair of samples in the data matrix form a lower triangular 'sample similarity matrix'.

Data transformation

Clarke (1993) and Clarke and Warwick (1994) warn that similarities calculated on the original data matrix ".....will typically lead to shallow interpretation...." Clarke (1993) because they will be overdominated by a small number of highly abundant species. The calculated similarities will therefore fail to reflect the similarity of the overall species assemblage. Although some similarity coefficients, for example the 'Canberra coefficient' Lance and Williams (1967), can weight the contribution of each species to adjust for this, they more often lead to the overdomination of the similarity by a large number of rare species, of no real significance. A balanced compromise can be achieved by applying the Bray-Curtis similarity coefficient to transformed data. This approach ensures that all species contribute something to the definition of similarity whilst retention of information on the relative abundance of the species ensures that more common species are given greater weight than rare ones. (Clarke, 1993; Clarke and Warwick, 1994). The same authors conclude that the most practical choice of transformation is a 4th root transformation ($y^*=y^{0.25}$ ) which essentially reduces the original data to approximately a six point scale where 0 = absent, 1 = one individual, 2 = handful, 3 = sizeable number, 4 = abundant, ≥5 = very abundant. All the multivariate analyses presented in this chapter employ this transformation.

MDS

The starting point for MDS is the sample similarity or dissimilarity matrix. The MDS algorithm uses an iterative procedure to construct an ordination plot that satisfies, as closely as possible, the dissimilarity ($\delta$ ) relations between the samples (where $\delta$ is simply the complement of the similarity ($S$)) by minimising the 'stress' value defined as:

$$stress = \frac{\sum_{j}^{n}\sum_{k}^{n}(d_{jk} - \hat{d}_{jk})^2}{\sum_{j}^{n}\sum_{k}^{n} d_{jk}^2} \quad (2$$

where

$d_{jk}$ = the distance between the $j$th and $k$th sample points on the ordination

$\hat{d}_{jk}$ = the distance corresponding to a dissimilarity of $\delta_{jk}$ predicted from a non-parametric regression of $d_{jk}$ on $\delta_{jk}$ for a given sample configuration.

*if* $d_{jk} = \hat{d}_{jk}$ for all the $n$ ($n$-1)/2 possible distances in the similarity matrix, then the stress is zero.

In order to ensure that the global minimum of the stress function was achieved, the MDS analysis was always repeated six times, starting with different random positions of samples in the initial configuration. If the same lowest stress solution re-appeared from these different starting configurations, then it was concluded that this was the best solution. The final computed stress value can be thought of as a good indicator of the adequacy of the MDS representation. Based upon empirical evidence and simulation studies of stress values, Clarke and Warwick (1994) have proposed the following guidelines for interpreting stress values:

Table 2.2 Guidelines for interpreting stress values.

| Stress value | Interpretation |
|---|---|
| < 0.05 | Gives an excellent representation with no prospect of misinterpretation. |

| Stress value | Interpretation |
|---|---|
| <0.1 | Corresponds to a good ordination with no real prospect of a mis-leading interpretation. |
| <0.2 | Still gives a potentially useful picture, though for values at the upper end of this range, too much reliance should not be placed on the detail of the plot. |
| 0.3 | Indicates that the points are close to being arbitrarily placed in the ordination space. |

The MDS ordination provides a graphical description of the relationships between the species assemblages at the various samples as described in Section 2.2. Visual examination of these relationships for evidence of replicate groupings, provides an informal means to test hypotheses, identified *a priori*, regarding the species assemblages at the groups of sites, samples or conditions.

ANOSIM - testing for differences between groups of samples/sites

When sample or site groupings are clearly evident, the informal test outlined above, may be sufficient to test hypotheses regarding sample groups. When differences between sample groups are less clear, a formal statistical test is required. Parametric tests based around multivariate analysis of variance (MANOVA) are unsuitable because their assumptions cannot be satisfied for typical multispecies abundance or biomass data. This is mainly due to the dominance of zero values in the species / sites matrix which even after transformation would not reduce to approximate (multivariate) normality (Clarke and Warwick, 1994). Seventy-five-percent of the entries in the data matrix used for this analysis are zero (see Table A2.1). Instead, a non-parametric permutation test was used, applied to the (rank) similarity matrix underlying the ordination. This 'ANOSIM' test (analysis of similarity) uses a randomisation approach to generate significance level, analogous to Monte Carlo tests. Null hypotheses are tested in three stages. Firstly, a 'test statistic' ($R$) is computed from:

$$R = \frac{(\overline{r_B} - \overline{r_W})}{\left(\frac{M}{2}\right)} \quad (3)$$

where

$\overline{r}_w$ = average rank similarity among replicates within the groups

$\overline{r}_B$ = average rank similarity from all pairs of replicates between different groups

where $M$ is calculated from:

$$M = \frac{n(n-1)}{2} \quad (4)$$

where $n$ is the total number of sites/samples under consideration.

$R = 1$ if all the replicates within a group of sites are more similar to each other than any replicates from other groups of sites. $R$ will tend to zero as similarities between and within groups become the same on average; $R$ will always lie between -1 and 1 (Clarke and Warwick 1994). Although the $R$ statistic provides a useful comparative measure of the degree of separation of groups of sites, it is more important to know whether it is significantly different from zero. The second stage of the test is therefore to recompute the test statistic under permutations by randomly re-labelling all the sites/samples, ensuring that all possible allocations of labels to the samples/sites are examined. The number of distinct ways of permuting the labels ($P$) for $n$ samples/sites within each $g$ groups is given by:

$$P = \frac{(gn)!}{[(n!)^g \, g!]} \quad (5)$$

Finally, the significance level is calculated as the percentage number of times the originally calculated value of the $R$ is exceeded. If the value is exceeded for less than 5% of the relabellings, then the null hypothesis is rejected. Clearly, the maximum attainable significance level of this type of test will depend upon the number

of possible permutations. At least 20 permutations are required to test at the 5% significance level.

The above test is referred to by Clarke and Warwick (1994) as a 'global' test, indicating that there are differences between groups of samples or sites. If only two groups are being tested, then the analysis finishes here, but when three or more groups are present, 'pairwise' testing is required. This is achieved by extracting and re-ranking the similarities for each pair of groups of sites and repeating the test procedure outlined above. However, it must be borne in mind that if many such tests are performed, the risk of committing a Type 1 error will cumulate in a fashion analogous to applying two sample *t*-tests to attack a multisample hypothesis. In this case, the chance of committing a Type 1 error is 13% for three means and 21% for four means for a critical value of *t* at $\alpha = 5\%$. This problem may be overcome using multiple comparison tests (see Zar, 1984 for further details). Unfortunately, no such solutions are possible here, so Clark and Warwick (1994) recommend exercising "..... appropriate caution in interpretation".

Multiple pairwise comparisons were, however, used only to provide guidance for pooling similar sites across geographical regions and habitat type in an attempt to improve the potential power of the permutation tests. The impact of the FCDI schemes on the assemblages was ultimately tested using only two groups of sites representing conditions inside and outside the FCDI schemes.

Indicator Species Analysis - determining species responsible for sample (site) groupings

The species responsible for site groupings were determined by computing the average contribution ($\bar{\delta}_i$) of each species to the overall average dissimilarity ($\bar{\delta}$) between all pairs of inter-group sites. Algebraically, if $\delta_{jk}(i)$ is the contribution of the *i*th species to the dissimilarity between two samples/sites then:

$$\delta_{jk}(i) = 100.\left( \frac{|y_{ij} - y_{ik}|}{\sum_{i=1}^{p}(y_{ij} + y_{ik})} \right) \qquad (6)$$

$\delta_{jk}(i)$ is then averaged over all pairs ($j$,$k$) with $j$ in the first group and $k$ in the second to give $\bar{\delta}_i$ (Clarke and Warwick, 1994).

The standard deviations SD($\delta_i$) of the $\delta_{jk}(i)$ values were also calculated as a measure of how consistently a species contributes to $\bar{\delta}_i$ across all pairs of sites. The ratio $\bar{\delta}_i$ /SD($\delta_i$) provides a useful measure of not only how much the $i$th species contributes to the dissimilarity between groups, but also how consistently it does so. Species with high ratios are therefore good discriminating species (Clarke and Warwick, 1994). The percentage and cumulative percentage average dissimilarity ($\bar{\delta}_i$) between the groups that is contributed by the $i$th species were calculated to aid interpretation.

Linking with environmental variables

Multivariate ecological data are often matched with a suite of environmental variables describing the physio-chemical properties of each replicate or sampling site (eg water depth, substrate, contaminant levels etc), which may be used to help explain the observed biological pattern.

Water quality parameters; dissolved oxygen concentration, conductivity, total dissolved solids, pH, transparency and water temperature were recorded each month by FAP 17 but only for a selected number of sites. No major differences where detected inside and outside the FCDI schemes with the exception of transparency which was generally higher inside. Fishing intensity, measured as standardised effort for dominant gear types[3] per unit area, (gear hrs $ha^{-1}$) was calculated for sites inside and outside FCDI schemes wherever possible by FAP17 for the period March 1993 to February 1994. Often, however, gear usage and catch rates were very different inside and outside which precluded the estimation of standardised effort (FAP17, 1994).

Analytical Approach

(Dis)similarities between species assemblages caught from all pristine sites were first

[3] Defined as gears that took at least 90% of the annual catch

examined to determine whether or not habitat type and/or geographical location are important factors influencing these assemblages. If no differences existed, then sites within these two strata were 'pooled' to increase the number of replicates available for the comparison of assemblages at modified and pristine sites. When differences existed, separate comparisons were performed on the relevant region and habitat combinations. Partitioning of assemblages according to different habitat to allow detailed interpretation of environmental impacts in large heterogenous areas has been carried out by Omi *et al*, 1979; Hawkes *et al* (1986) as cited by Barrella and Petrere (1994).

A two-factor crossed ANOSIM described by Clarke (1993) and Clarke and Warwick (1994) was used to test two null hypotheses regarding the observed pattern in the MDS ordination of the pristine sites:

$H_1$: There are no differences in species assemblages between different habitat types (allowing for the fact that there may be differences between regions).

$H_2$: There are no differences in species assemblages between different geographical regions (allowing for the fact that there may be differences between habitat types).

To test the first null hypothesis, an $R$ statistic was calculated for each separate region using equation 2.4, as if for a simple one-way test for differences among habitat types, and the resulting values averaged to give $\overline{R}$. The significance level of the test was determined by the number of times this value was exceeded during simultaneous re-orderings of each habitat label within each region.

If the first hypothesis is rejected, then the second can be tested allowing for the fact that there are differences in species composition between habitat types. This is achieved by reversing the role of the factors. In this case $\overline{R}$ is the average of the values of $R$ calculated for each habitat type and the permutation distribution is generated from simultaneous relabellings of the region labels. When three or more levels are present within each factor, pairwise testing is required. This is achieved in a manner analogous to the one-way ANOSIM, where $\overline{R}$ is calculated from the extracted and re-ranked similarities for each pair of groups of sites.

Having determined which (if any) site habitat/region combinations could be legitimately pooled, MDS was used to compare (dis)similarities in the species assemblages caught from modified and pristine sites. The null hypothesis ($H_o$) that there are no differences in species assemblages between the two conditions was then tested with the one-way ANOSIM test. Indicator species analysis was then applied to those comparisons which exhibited statistically significant differences at the 5% level or below to assess which species were responsible for the observed pattern. The monetary value of the assemblages at these groups of sites was also compared to evaluate the economic impact of FCDI schemes. These values were derived from the average abundance of the species in each group and the regional average annual price (TK/kg) of each species recorded by FAP17 (FAP17, 1995 vol.20).

The PRIMER (Plymouth Routines in Multivariate Ecological Research) program (Clarke and Warwick, 1994) was used for the MDS, ANOSIM and indicator species analyses.

## 2.4 Results

Figure 2.5a shows the MDS ordination for all pristine sites labelled by habitat type and geographical location. Careful examination reveals three overlapping clusters of sites, separated according to habitat type; main and secondary river to the left; floodplain/beel to the right and canal towards the bottom right hand corner. Simultaneous clustering of sites by region is also evident, shown by separation along the y-axis. This separation is perhaps less pronounced for sites in the NW and NC region. These patterns indicate that both habitat type and geographic location influence species assemblages.

Unfortunately this hypothesis could not be tested using all the sites shown in Figure 2.5a because the two-way crossed ANOSIM test described above, requires at least one replicate within each factor combination (habitat/region). Of the 16 possible factor combinations, three contained no replicates. These were main river in the north east, canal in the north east and floodplain/beel in the south west. Canal and main river sites, which comprise only a relatively small proportion (35%) of the total number of pristine sites in the data set, were therefore excluded from this part of the analysis. Similarly all data from the SW region were omitted due to the absence of replicate sites from floodplain/beel, a habitat regarded as particularly important to this research. These three habitat/region stratifications were therefore retained for the modified/pristine site comparisons.

The MDS ordination for the remaining pristine habitat/region combinations is displayed in Figure 2.5b. The same pattern as that described for Figure 2.5a again emerges , though with greater clarity, showing differences in species assemblages between both floodplain/beel and secondary river habitat type and between the three geographical regions. The results of the two-way ANOSIM test for these sites are given in Table 2.3. Both null hypotheses were decisively rejected at a significance level of 0% indicating significant species dissimilarities between both habitat type and geographical location. The pairwise test did however indicate that the hypothesis of no differences in species assemblages between sites in the NC and NW could only be rejected at a $P < 10\%$ level.

Figure 2.5 (a) MDS ordination for all pristine sites (stress=0.15). (b) MDS ordination for habitat/region combinations containing at least one replicate (stress=0.13). ❍ - Floodplain/Beel sites; _ - Secondary rivers; _-Main Rivers; □-Canals. Fill style indicates geographic location of sampling site where open = NC, solid = NE; hatched=NW and crosshatched =SW.

Table 2.3 Results from the two-way crossed ANOSIM test for differences between habitat and region groups (clusters) of sites.

$H_1$: There are no differences in species assemblages between different habitat types (allowing for the fact that there may be differences between regions).

$H_2$: There are no differences in species assemblages between different geographical regions (allowing for the fact that there may be differences between habitat types).

$H_1$:

Sample statistic ($\overline{R}$ ): 0.517

Number of permutations: 20000 (RANDOM SAMPLE FROM APPROX 1.514D+06)

Number of permuted statistics greater than or equal $\overline{R}$: 0

Significance level of sample statistic: 0.0%

$H_2$:
Sample statistic ( $\bar{R}$) : 0.605
Number of permutations: 20000 (RANDOM SAMPLE FROM APPROX 1.249D+09)
Number of permuted statistics greater than or equal to $\bar{R}$: 0
Significance level of sample statistic: 0.0%

| Groups | $\bar{R}$ value | Possible permutations | Permutations used | Significant statistics | Significance level |
|---|---|---|---|---|---|
| NC, NE | 0.789 | $2.28 \times 10^5$ | 5000 | 0 | 0.0% |
| NC, NW | 0.267 | 1155 | 1155 | 102 | 8.8% |
| NE, NW | 0.404 | 210 | 210 | 7 | 3.3% |

Nonetheless, given that the argument here is whether "to pool" or "not to pool", it would be prudent to assume that species assemblages do differ among habitat types and among all regions. Separate modified/pristine site comparisons of species assemblages were therefore carried out for each habitat/region combination.

MDS ordinations for these combinations are shown in Figure 2.6. Habitat types are depicted by the same symbols as those used in Figure 2.5. Open symbols represent pristine (outside) sites and solid symbols donate modified (inside) sites. Main rivers in all four regions, secondary rivers and canals in the NE, canals in the NW and secondary rivers and floodplain/beel habitats in the SW could not be included due to the absence of

one or more replicates in one or both modified or pristine site categories. The calculated stress values given in the figure legend suggest that all the ordinations provide excellent or good representations of the relationships between the sites with no real prospect of misrepresentation.

The results of the ANOSIM tests for each ordination are summarised in Table 2.4 which includes the calculated *R* statistic, the number of possible permutations, the number of significant statistics, the significance level (P) and the maximum attainable significance level.

NC region

Examination of the first row of ordinations in Figure 2.6 indicate that species assemblages caught from modified and pristine floodplain/beel habitat are not dissimilar since the two modified sites are located well within the 'spread' of the pristine sites. This inference is supported by the results of the ANOSIM test (Table 2.4) which shows a 31% chance of committing a Type I error. The ordination for the canal habitat does show some weak evidence of assemblage dissimilarity between the site conditions though because there was only a single replicate representing the modified condition, and the overall number of replicates was low, the null hypothesis could not be rejected at the 5% level. The calculated significance level was, however, equal to the maximum attainable significance level.

Figure 2.6 MDS ordinations for each habitat/region combination. Symbols as for Figure 2.5. Open symbols indicate pristine (outside) sites, solid indicate modified (inside) sites. Stress values for each ordination from left to right and top to bottom; 0.08, 0.03, 0.12, 0.00, 0.03, 0.00.

Table 2.4 Summary of the results of the one-way ANOSIM to test the null hypothesis

that there are no differences in species assemblages between modified and pristine sites of similar habitat type within each geographic region.

$H_o$: There are no differences in species assemblages between modified and pristine sites of the same habitat type and geographic region.

| Region | Habitat | FCD/I | DOR | *R* stat. | Permutations | Significant statistics | Significance level (*p*) | $H_o$: | Max. attainable significance level |
|---|---|---|---|---|---|---|---|---|---|
| NC | FB | CPP | N | 0.15 | 45 | 14 | 31.1 % | Accept | 7.0 % |
| NC | C | CPP | N | 0.50 | 5 | 1 | 20.0 % | Accept | 20.0 % |
| NE | FB | MIP<br>SHP | P<br>P | 0.44 | 126 | 1 | 0.8 % | Reject | 0.8% |
| NW | SR | PIRDP | F | 0.42 | 5 | 2 | 40.0% | Accept | 20.0 % |
| NW | FB | PIRDP<br>PB | F | 0.59 | 84 | 1 | 1.2 % | Reject | 1.2 % |
| SW | C | CFP<br>SBP | P<br>F | 0.43 | 15 | 2 | 13.3 % | Accept | 6.6 % |

DOR - degree of hydraulic regulation: N -none; P -partial; F -full.

NE region

Only floodplain/beel habitat could be examined in this region due to the absence of modified or pristine sites in the other two habitat categories. The ordination for this combination shows separation of modified and pristine sites along the y-axis indicating assemblage dissimilarity between the two groups. The ANOSIM test also rejected the null hypothesis at the 0.8% level. The modified site in the centre of the ordination appears less dissimilar to the pristine sites than the others. The pristine sites are also quite widely dispersed relative to the modified sites indicating relatively lower assemblage similarities within this group.

NW region

Similar to the canal habitat in the NE, the ordination and the calculated *R* statistic for secondary river habitat in the NW region indicate a degree of separation between the two site conditions. However, the ANOSIM tested failed to reject the null hypothesis (*P* = 40%). The ordination for floodplain/beel habitat shows an unequivocal dissimilarity between pristine and modified sites. The ANOSIM test also decisively rejected the null hypothesis at the 1.2% level (the maximum attainable significance level).

SW region

The ordination for canal habitat in the SW region shows that one of the modified sites is similar, and the other very dissimilar, to the pristine sites. The *R* statistic (*R* = 0.43) indicates some degree of separation between the two groups of sites though the ANOSIM test rejected the null hypothesis only at the 13.3% level (maximum attainable significance level =6.6%).

Indicator species analysis

Table 2.5 summaries the results of the indicator species analysis for the floodplain/beel habitat in the NW region. The table contains the average abundance (kg/100hrs of fishing effort) of each species for both site conditions, including $\bar{\_}_i$, $\bar{\_}_i$/SD $\bar{\_}_i$, $\%\bar{\_}_i$ and cumulative $\%\bar{\_}_i$. A comparison of the average abundance of each species is graphically presented in Figure 2.7. Species are arranged from top to bottom in descending order of their $\bar{\_}_i$/SD $\bar{\_}_i$ ratio. To assist interpretation, only those species contributing to 75% of the

cumulative average dissimilarity (column 7 in Table 2.5) are shown.

Considering only those which contributed to 75% of the dissimilarity between the two site conditions, species that were consistently absent (<0.00kg/100hrs) or virtually absent (<0.1kg/100hrs) from modified sites but present in pristine sites, in descending order of their $\bar{}_i$/SD $\bar{}_i$ ratio were *Nemachilus botia*, *Pseudeutropius atherinoides, Clupisoma garua, Mystus bleekeri, Ailia coila, Silonia silondia, Rhinomugil corsula*, *Oxygaster gora*, *Catla catla, Labeo bata*, *Heteropneustes fossilis, Gagata youssoufi, Labeo calbasu*, and *Ompok pabda*. Species that contributed significantly (>2kg/100hrs) to the overall abundance at pristine sites which were substantially (>50%) less abundant at modified sites were *Hilsha ilisha, Glossogobius girius, Gudusia chapra, Corica soborna, Labeo rohita, Labeo guntea, Mystus vittatus, Puntius sophore, Cirrhinus reba, Cirrhinus mrigala and Wallago attu*. Based upon price data recorded at markets in the NW region by FAP17 (FAP17 1993 vol20), the mean unit value of these species is TK45.6/kg.

Conversely, species that were consistently absent (<0.00kg/100hrs) or virtually absent (<0.1kg/100hrs) from pristine sites but present in modified sites, in descending order of their $\bar{}_i$/SD $\bar{}_i$ ratio were *Puntius gelius, Puntius phutunio* and *Brachygobius nunus*. However, in each case their contribution to the average abundance at modified sites was not significant (<2kg/100hrs). Species that did contribute significantly (>2kg/100hrs) to the overall abundance at modified sites which were substantially (>50%) less abundant at pristine sites were *Xenentodon cancila, Salmostoma phulo*, *Mastacembelus pancalus*, *Chanda nama* and *Chanda baculis.* These species have a unit value of only TK27/kg.

Overall, the unit value of the assemblage in pristine sites (TK 32/kg) is 25% greater than modified sites (TK 25.5/kg).

Table 2.5 Results of the indicator species analysis for floodplain beel habitat in the NW region where full flood control is present.

| | Abundance (kg/100hrs) | | | | | | Price | Value (TK) | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Pristine | Modified | $\bar{\lambda}_i$ | $\bar{\lambda}_i/SD\ \bar{\lambda}_i$ | % | cum% | (TK/kg) | Pristine | Modified |
| *X.cancila* | 1.97 | 38.99 | 1.54 | 1.36 | 3.23 | 3.23 | 24.76 | 48.78 | 965.39 |
| *P.atherinoides* | 2.20 | 0 | 1.28 | 3.89 | 2.69 | 5.93 | 45.86 | 100.89 | 0.00 |
| *R.corsula* | 2.69 | 0 | 1.18 | 2.26 | 2.49 | 8.41 | 28.23 | 75.93 | 0.00 |
| *A.coila* | 1.68 | 0 | 1.17 | 2.90 | 2.45 | 10.87 | 53.39 | 89.69 | 0.00 |
| *M.bleekeri* | 1.76 | 0.01 | 1.15 | 3.07 | 2.42 | 13.28 | 58.18 | 102.40 | 0.58 |
| *H.ilisha* | 16.89 | 0.98 | 1.14 | 1.49 | 2.39 | 15.67 | 55.17 | 931.82 | 54.07 |
| *L.bata* | 3.10 | 0 | 1.14 | 1.51 | 2.38 | 18.06 | 28.72 | 89.02 | 0.00 |
| *P.sophore* | 20.99 | 11.72 | 1.09 | 1.17 | 2.30 | 20.36 | 24.76 | 519.71 | 290.19 |
| *S.phulo* | 9.09 | 51.37 | 1.08 | 2.06 | 2.27 | 22.63 | 26.56 | 241.43 | 1364.39 |
| *M.pancalus* | 1.87 | 15.19 | 1.04 | 2.29 | 2.17 | 24.8 | 39.00 | 72.93 | 592.41 |
| *L.rohita* | 4.65 | 0.47 | 1.02 | 1.33 | 2.15 | 26.95 | 57.43 | 267.05 | 26.99 |
| *C.garua* | 0.79 | 0 | 0.97 | 3.42 | 2.04 | 28.99 | 38.89 | 30.73 | 0.00 |
| *C.catla* | 2.09 | 0.06 | 0.97 | 1.54 | 2.04 | 31.03 | 44.22 | 92.42 | 2.65 |
| *S.silondia* | 0.80 | 0 | 0.97 | 2.56 | 2.03 | 33.06 | 89.84 | 71.87 | 0.00 |
| *C.reba* | 18.39 | 2.29 | 0.94 | 0.99 | 1.98 | 35.04 | 41.92 | 770.98 | 96.01 |
| *C.nama* | 21.71 | 28.68 | 0.92 | 1.34 | 1.94 | 36.98 | 19.83 | 430.51 | 568.72 |
| *G.youssoufi* | 1.69 | 0 | 0.91 | 1.20 | 1.91 | 38.89 | 44.49 | 75.19 | 0.00 |
| *C.punctatus* | 1.73 | 3.14 | 0.89 | 1.28 | 1.87 | 40.76 | 23.40 | 40.48 | 73.48 |
| *C.baculis* | 1.47 | 7.08 | 0.86 | 1.34 | 1.81 | 42.57 | 20.80 | 30.58 | 147.26 |
| *L.guntea* | 3.20 | 1.05 | 0.85 | 1.26 | 1.79 | 44.36 | 28.72 | 91.89 | 30.15 |
| *Prawn* | 28.31 | 23.00 | 0.85 | 1.13 | 1.79 | 46.14 | 19.57 | 554.03 | 450.11 |
| *M.armatus* | 1.70 | 0.16 | 0.83 | 1.37 | 1.75 | 47.89 | 48.28 | 82.08 | 7.73 |
| *G.giurus* | 13.55 | 5.21 | 0.82 | 1.39 | 1.72 | 49.61 | 35.41 | 479.85 | 184.50 |
| *P.gelius* | 0.04 | 1.38 | 0.78 | 1.98 | 1.64 | 51.25 | 24.76 | 0.99 | 34.17 |
| *C.mrigala* | 2.50 | 0.44 | 0.78 | 0.91 | 1.63 | 52.88 | 37.76 | 94.41 | 16.62 |
| *L.calbasu* | 0.93 | 0 | 0.77 | 1.18 | 1.62 | 54.51 | 37.76 | 35.12 | 0.00 |
| *M.tengra* | 0.10 | 1.94 | 0.77 | 1.62 | 1.61 | 56.12 | 58.18 | 5.82 | 112.87 |
| *O.gora* | 0.76 | 0.02 | 0.76 | 1.67 | 1.60 | 57.72 | 34.22 | 26.01 | 0.68 |
| *G.chapra* | 15.91 | 7.98 | 0.75 | 1.38 | 1.57 | 59.29 | 23.80 | 378.59 | 189.89 |
| *P.phutunio* | 0.01 | 0.68 | 0.71 | 1.59 | 1.50 | 60.78 | 24.76 | 0.25 | 16.84 |
| *C.fasciatus* | 0.88 | 1.66 | 0.70 | 1.35 | 1.47 | 62.26 | 24.76 | 21.79 | 41.10 |
| *N.botia* | 0.17 | 0 | 0.70 | 4.21 | 1.46 | 63.72 | 35.41 | 6.02 | 0.00 |
| *O.pabda* | 1.31 | 0.02 | 0.69 | 1.09 | 1.46 | 65.17 | 100.80 | 132.04 | 2.02 |
| *M.vittatus* | 2.89 | 1.59 | 0.69 | 1.22 | 1.45 | 66.62 | 45.86 | 132.54 | 72.92 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *M.aor* | 0.52 | 0.36 | 0.69 | 1.33 | 1.44 | 68.06 | 98.06 | 50.99 | 35.30 |
| *W.attu* | 2.30 | 0.47 | 0.67 | 0.79 | 1.40 | 69.46 | 54.78 | 125.99 | 25.75 |
| *C.soborna* | 2.93 | 0.55 | 0.65 | 1.35 | 1.35 | 70.81 | 34.00 | 99.61 | 18.70 |
| *B.nanus* | 0 | 0.34 | 0.61 | 1.34 | 1.29 | 72.1 | 35.41 | 0.00 | 12.04 |
| *T.cutcutia* | 0.23 | 1.67 | 0.61 | 1.24 | 1.29 | 73.39 | - | - | - |
| *H.fossilis* | 0.40 | 0.06 | 0.57 | 1.27 | 1.21 | 74.6 | 60.69 | 24.27 | 3.64 |
| *E.danricus* | 0.57 | 0.53 | 0.57 | 1.29 | 1.20 | 75.8 | 17.83 | 10.16 | 9.45 |
| *D.devario* | 0.12 | 0 | 0.57 | 2.09 | 1.20 | 76.99 | 35.41 | 4.25 | 0.00 |
| *B.dario* | 0.27 | 0.15 | 0.57 | 1.28 | 1.19 | 78.18 | 34.22 | 9.24 | 5.13 |
| *C.lalius* | 0.51 | 0.30 | 0.56 | 1.26 | 1.17 | 79.35 | 15.86 | 8.09 | 4.76 |
| *M.cavasius* | 0.15 | 0.22 | 0.54 | 1.41 | 1.13 | 80.48 | 58.18 | 8.73 | 12.80 |
| *S.bacaila* | 0.52 | 0.19 | 0.53 | 1.31 | 1.11 | 81.59 | 26.56 | 13.81 | 5.05 |
| *M.aculeatus* | 1.52 | 1.47 | 0.52 | 1.08 | 1.09 | 82.69 | - | - | - |
| *C.ranga* | 8.56 | 15.41 | 0.49 | 1.62 | 1.03 | 83.71 | 19.83 | 169.74 | 305.58 |
| *E.vacha* | 0.12 | 0 | 0.46 | 1.29 | 0.97 | 84.69 | 41.63 | 5.00 | 0.00 |
| *S.gongota* | 0.12 | 0 | 0.46 | 1.30 | 0.97 | 85.65 | 35.41 | 4.25 | 0.00 |
| *A.mola* | 0.25 | 0.33 | 0.44 | 1.47 | 0.93 | 86.59 | 47.04 | 11.76 | 15.52 |
| *O.bimaculatus* | 0.09 | 0.05 | 0.42 | 1.25 | 0.88 | 87.46 | 100.80 | 9.07 | 5.04 |
| *P.conchonius* | 4.19 | 11.13 | 0.41 | 1.30 | 0.85 | 88.32 | 24.76 | 103.74 | 275.58 |
| *C.sota* | 0.25 | 0.09 | 0.40 | 0.79 | 0.84 | 89.16 | 15.86 | 3.97 | 1.43 |
| *C.lalius* | 0 | 0.27 | 0.38 | 0.65 | 0.80 | 89.96 | 15.86 | 0.00 | 4.28 |
| *R.cotio* | 0.04 | 0 | 0.38 | 1.35 | 0.80 | 90.76 | 45.86 | 1.83 | 0.00 |
| *L.boga* | 0.18 | 0.06 | 0.37 | 0.79 | 0.77 | 91.53 | 28.72 | 5.17 | 1.72 |
| *J.coitor* | 0.29 | 0 | 0.35 | 0.68 | 0.74 | 92.28 | 34.22 | 9.92 | 0.00 |
| *S.phasa* | 0.14 | 0 | 0.33 | 0.68 | 0.69 | 92.97 | 23.80 | 3.33 | 0.00 |
| *P.ticto* | 0 | 0.08 | 0.32 | 0.87 | 0.68 | 93.65 | 11.14 | 0.00 | 0.89 |
| *N.zonatus* | 0.19 | 0 | 0.32 | 0.68 | 0.67 | 94.31 | 35.41 | 6.73 | 0.00 |
| *G.manminna* | 0 | 0.11 | 0.31 | 0.91 | 0.65 | 94.96 | 34.22 | 0.00 | 3.76 |
| *B.badis* | 0.35 | 0.27 | 0.30 | 0.83 | 0.63 | 95.59 | 34.22 | 11.98 | 9.24 |
| *C.marulius* | 0 | 1.35 | 0.27 | 0.43 | 0.57 | 96.16 | 36.40 | 0.00 | 49.14 |
| *Mparsia* | 0.01 | 0.09 | 0.27 | 0.77 | 0.57 | 96.72 | - | - | - |
| *C.orientalis* | 0.07 | 0 | 0.25 | 0.68 | 0.53 | 97.25 | 36.40 | 2.55 | 0.00 |
| *B.evez* | 0.03 | 0 | 0.20 | 0.68 | 0.43 | 97.68 | 26.56 | 0.80 | 0.00 |
| *B.batasio* | 0.02 | 0 | 0.18 | 0.68 | 0.38 | 98.07 | 34.22 | 0.68 | 0.00 |
| *P.boro* | 0 | 0.10 | 0.16 | 0.43 | 0.34 | 98.41 | 34.22 | 0.00 | 3.42 |
| *M.rosenbergii* | 0.01 | 0 | 0.15 | 0.68 | 0.31 | 98.72 | 193.33 | 1.93 | 0.00 |
| *B.boddarti* | 0 | 0.05 | 0.14 | 0.43 | 0.30 | 99.02 | - | - | - |
| *C.latius* | 0.01 | 0 | 0.14 | 0.68 | 0.30 | 99.32 | 35.41 | 0.35 | 0.00 |
| *M.piceus* | 0 | 0 | 0.13 | 0.68 | 0.27 | 99.59 | 34.22 | 0.00 | 0.00 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *A.morar* | 0 | 0 | 0.12 | 0.68 | 0.25 | 99.84 | 51.34 | 0.00 | 0.00 |
| **Total** | **212.78** | **240.81** | | | | | | **6831.79** | **6149.96** |

Figure 2.7 Average abundance of species from modified and pristine floodplain/beel sites in the NW region. Species are arranged from top to bottom in descending order of their $\bar{}_{i}$/SD $\bar{}_{i}$ ratio. Only those species contributing to 75% of the cumulative average dissimilarity (column 7 in Table 2.5) are shown.

Table 2.6 and Figure 2.8 summarise the results of the indicator species analysis for the NE region in the same format used for the NW region. Using the same definitions as for the NW region, species that were absent or virtually absent at modified sites, but present at pristine sites, were *Mystus bleekeri, Wallago attu* and *Somileptes gongota*. Significantly lower abundances at modified compared with pristine sites were found for *Puntius conchonius,* prawn species, *Glossogobius giurus, Puntius ticto, Notopterus notopterus, Corica soborna, Tetraodon cutcutia, Salmostoma bacaila, Mystus tengra, Mystus aor, Mastacembelis armatus, Pellona ditchela, Hypophthalmichthys molitrix, Mystus cavasius, Chandramara chandramara, Gudusia chapra* and *Clupisoma garua.* These species have a unit value of 36.5TK/kg.

Species that were absent or virtually absent at pristine sites, but present at modified sites were *Colisa lalius, Colisa sota* and *Hilsha ilisha*. Finally, species which exhibited significantly lower abundances at pristine compared with modified sites were *rasbora daniconius, colisa fasciatus, Nandus nandus, Xenentodon cancila, Ablypharyngodon mola, Puntius gelius, Salmostoma phulo, Chanda baculis, Badis badis, Chanda nama, Puntius phutunio* and *Puntius chola*. The mean unit value of these species is TK26.5/kg.

Overall, the unit value of the assemblage in pristine sites in the NE region (TK26/kg) is only marginally greater (8%) than in modified sites (TK24/kg).

Linking with environmental variables

Fishing intensity was consistently and significantly higher inside the FCDI schemes in

both the NE and NW regions (Table 2.7). Standardised fishing intensity could not be calculated for Chalan Beel Polder B scheme, but for the most important gear types the annual effort deployed per hectare of floodplain was 2-5 times higher inside the scheme compared to outside.

Table 2.6 Results of the indicator species analysis for floodplain beel habitat in the NE region.

| | Abundance (kg/100hrs) | | | | | | Price | Value (TK) | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Pristine | Modified | $\bar{}_i$ | $\bar{}_i$/SD $\bar{}_i$ | % | cum% | (TK/kg) | Pristine | Modified |
| *P.conchonius* | 217.96 | 7.45 | 1.90 | 1.17 | 3.80 | 3.8 | 25.45 | 5547.08 | 189.60 |
| *Prawn* | 384.49 | 107.20 | 1.42 | 1.38 | 2.84 | 6.65 | 17.36 | 6674.75 | 1860.99 |
| *G.giurus* | 48.32 | 4.28 | 1.21 | 2.12 | 2.42 | 9.07 | 30.43 | 1470.22 | 130.23 |
| *P.ticto* | 40.10 | 3.22 | 1.19 | 0.88 | 2.39 | 11.46 | 11.45 | 459.25 | 36.88 |
| *N.notopterus* | 53.95 | 7.71 | 1.18 | 1.33 | 2.36 | 13.82 | 58.11 | 3135.29 | 448.07 |
| *R.daniconius* | 0.48 | 31.57 | 1.15 | 1.48 | 2.30 | 16.12 | 18.07 | 8.67 | 570.45 |
| *C.soborna* | 19.65 | 0.44 | 1.13 | 1.42 | 2.25 | 18.38 | 29.21 | 573.97 | 12.85 |
| *T.cutcutia* | 71.27 | 8.01 | 1.12 | 1.45 | 2.23 | 20.61 | - | - | - |
| *C.fasciatus* | 1.07 | 15.38 | 1.08 | 1.84 | 2.15 | 22.76 | 17.90 | 19.15 | 275.24 |
| *C.lalius* | 0 | 10.22 | 1.08 | 1.72 | 2.15 | 24.92 | 17.90 | 0.00 | 182.90 |
| *N.nandus* | 12.27 | 17.16 | 1.07 | 1.43 | 2.13 | 27.05 | 38.18 | 468.41 | 655.08 |
| *S.bacaila* | 20.88 | 0.59 | 1.05 | 0.94 | 2.10 | 29.15 | 22.82 | 476.48 | 13.46 |
| *X.cancila* | 17.39 | 74.46 | 1.04 | 1.32 | 2.09 | 31.24 | 25.45 | 442.58 | 1895.01 |
| *M.bleekeri* | 10.16 | 0 | 1.04 | 1.33 | 2.09 | 33.33 | 39.65 | 402.80 | 0.00 |
| *A.mola* | 3.01 | 10.47 | 1.02 | 1.25 | 2.04 | 35.37 | 48.36 | 145.55 | 506.28 |
| *M.tengra* | 12.45 | 2.31 | 1.00 | 1.62 | 2.00 | 37.37 | 39.65 | 493.59 | 91.58 |
| *P.gelius* | 17.87 | 46.88 | 0.94 | 1.60 | 1.88 | 39.25 | 25.45 | 454.79 | 1193.10 |
| *S.phulo* | 10.97 | 42.49 | 0.94 | 1.14 | 1.88 | 41.13 | 22.82 | 250.34 | 969.62 |
| *P.terio* | 2.97 | 2.36 | 0.91 | 1.93 | 1.83 | 42.96 | 25.45 | 75.59 | 60.06 |
| *C.baculis* | 83.90 | 105.92 | 0.87 | 1.68 | 1.74 | 44.69 | 20.45 | 1715.92 | 2166.28 |
| *B.badis* | 1.06 | 2.53 | 0.85 | 1.69 | 1.70 | 46.4 | 23.32 | 24.72 | 59.00 |
| *M.pancalus* | 5.14 | 3.88 | 0.84 | 1.35 | 1.68 | 48.07 | 34.24 | 175.98 | 132.84 |
| *M.aor* | 7.01 | 0.26 | 0.82 | 1.03 | 1.63 | 49.7 | 96.57 | 676.96 | 25.11 |
| *M.armatus* | 3.43 | 0.40 | 0.79 | 1.37 | 1.58 | 51.28 | 49.63 | 170.22 | 19.85 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *H.ilisha* | 0 | 2.50 | 0.78 | 1.10 | 1.57 | 52.85 | 47.36 | 0.00 | 118.40 |
| *P.ditchela* | 10.61 | 0.97 | 0.77 | 0.74 | 1.54 | 54.39 | 23.32 | 247.43 | 22.62 |
| *C.nama* | 8.88 | 37.41 | 0.77 | 1.12 | 1.53 | 55.92 | 22.37 | 198.65 | 836.86 |
| *H.gaimardi* | 4.26 | 1.55 | 0.76 | 1.04 | 1.51 | 57.43 | 23.32 | 99.35 | 36.15 |
| *W.attu* | 6.24 | 0 | 0.75 | 0.94 | 1.50 | 58.93 | 53.95 | 336.65 | 0.00 |
| *C.marulius* | 4.30 | 2.85 | 0.74 | 1.01 | 1.48 | 60.42 | 35.79 | 153.90 | 102.00 |
| *P.phutunio* | 1.01 | 8.19 | 0.73 | 1.41 | 1.45 | 61.87 | 25.45 | 25.70 | 208.44 |
| *C.sota* | 0 | 1.19 | 0.73 | 1.72 | 1.45 | 63.33 | 17.90 | 0.00 | 21.30 |
| *N.maydelli* | 1.98 | 0.24 | 0.71 | 1.38 | 1.43 | 64.75 | 29.44 | 58.30 | 7.07 |
| *M.cavasius* | 11.56 | 3.00 | 0.69 | 0.71 | 1.39 | 66.14 | 39.65 | 458.30 | 118.94 |
| *S.gongota* | 2.58 | 0 | 0.69 | 0.94 | 1.38 | 67.52 | 30.43 | 78.50 | 0.00 |
| *C.chandramara* | 6.30 | 0.70 | 0.68 | 1.14 | 1.36 | 68.88 | 23.32 | 146.92 | 16.32 |
| *C.punctatus* | 2.05 | 2.37 | 0.68 | 1.23 | 1.35 | 70.23 | 23.01 | 47.17 | 54.53 |
| *P.chola* | 0.88 | 2.94 | 0.67 | 1.10 | 1.35 | 71.58 | 25.45 | 22.40 | 74.82 |
| *G.chapra* | 103.01 | 45.52 | 0.66 | 1.43 | 1.32 | 72.9 | 26.84 | 2765.20 | 1221.94 |
| *P.sophore* | 29.53 | 22.99 | 0.65 | 1.39 | 1.31 | 74.21 | 25.45 | 751.54 | 585.10 |
| *C.garua* | 2.56 | 0.23 | 0.59 | 0.92 | 1.19 | 75.39 | 38.30 | 98.06 | 8.81 |
| *H.molitrix* | 13.94 | 0 | 0.58 | 0.56 | 1.15 | 76.54 | 36.50 | 508.78 | 0.00 |
| *M.aculeatus* | 2.93 | 0.05 | 0.56 | 0.83 | 1.12 | 77.66 | 31.84 | 93.29 | 1.59 |
| *C.ranga* | 27.69 | 38.34 | 0.55 | 1.59 | 1.10 | 78.76 | 22.37 | 619.43 | 857.67 |
| *N.boti* | 1.54 | 0.01 | 0.53 | 0.88 | 1.06 | 79.82 | 30.43 | 46.86 | 0.30 |
| *C.striatus* | 3.99 | 0.35 | 0.51 | 0.75 | 1.01 | 80.83 | 51.13 | 204.01 | 17.90 |
| *B.dario* | 1.78 | 0.22 | 0.49 | 0.90 | 0.98 | 81.81 | 23.32 | 41.51 | 5.13 |
| *L.rohita* | 3.15 | 1.21 | 0.49 | 0.72 | 0.98 | 82.79 | 67.82 | 213.63 | 82.06 |
| *L.guntea* | 0.62 | 0.40 | 0.48 | 1.02 | 0.95 | 83.74 | 33.91 | 21.02 | 13.56 |
| *B.tengara* | 2.67 | 0 | 0.47 | 0.56 | 0.94 | 84.68 | 23.32 | 62.27 | 0.00 |
| *G.youssoufi* | 2.89 | 0 | 0.46 | 0.56 | 0.91 | 85.59 | 30.32 | 87.62 | 0.00 |
| *M.vittatus* | 1.47 | 0.06 | 0.46 | 0.95 | 0.91 | 86.51 | 39.65 | 58.28 | 2.38 |
| *C.reba* | 0.41 | 0 | 0.42 | 0.96 | 0.84 | 87.35 | 49.51 | 20.30 | 0.00 |
| *L.calbasu* | 1.49 | 0.14 | 0.42 | 0.74 | 0.84 | 88.19 | 46.80 | 69.73 | 6.55 |
| *Unknown* | 0.60 | 0 | 0.42 | 0.94 | 0.84 | 89.03 | - | - | - |
| *M.seenghala* | 0.93 | 0.41 | 0.41 | 0.73 | 0.82 | 89.85 | 39.65 | 36.87 | 16.25 |
| *O.pabda* | 3.28 | 0 | 0.40 | 0.56 | 0.80 | 90.65 | 99.27 | 325.60 | 0.00 |
| *H.fossilis* | 0.46 | 0.14 | 0.38 | 0.97 | 0.76 | 91.42 | 55.70 | 25.62 | 7.80 |
| *R.cotio* | 0.23 | 0.22 | 0.37 | 0.90 | 0.75 | 92.16 | 23.32 | 5.36 | 5.13 |
| *C.catla* | 0 | 3.22 | 0.37 | 0.48 | 0.74 | 92.91 | 52.22 | 0.00 | 168.15 |
| *C.battrachus* | 0 | 2.29 | 0.36 | 0.69 | 0.72 | 93.63 | 64.05 | 0.00 | 146.67 |
| *E.dandricus* | 0.08 | 1.52 | 0.34 | 0.74 | 0.68 | 94.31 | 18.32 | 1.47 | 27.85 |
| *C.chaca* | 2.27 | 0 | 0.34 | 0.56 | 0.67 | 94.98 | 34.98 | 79.41 | 0.00 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *A.testudineus* | 0 | 1.56 | 0.32 | 0.69 | 0.65 | 95.63 | 59.59 | 0.00 | 92.97 |
| *P.atherinoides* | 0.55 | 0 | 0.30 | 0.56 | 0.60 | 96.23 | 31.25 | 17.19 | 0.00 |
| *A.coila* | 0 | 0.65 | 0.25 | 0.48 | 0.50 | 96.73 | 36.38 | 0.00 | 23.65 |
| *B.nunus* | 0.53 | 0 | 0.23 | 0.56 | 0.47 | 97.2 | 30.43 | 16.13 | 0.00 |
| *P.boro* | 0.02 | 0.04 | 0.19 | 0.72 | 0.39 | 97.59 | 23.32 | 0.47 | 0.93 |
| *B.batasio* | 0 | 0.63 | 0.19 | 0.48 | 0.37 | 97.96 | 23.32 | 0.00 | 14.69 |
| *O.bimaculatus* | 0.13 | 0 | 0.17 | 0.56 | 0.33 | 98.3 | 99.27 | 12.90 | 0.00 |
| *C.nobolis* | 0 | 0.27 | 0.15 | 0.48 | 0.30 | 98.6 | - | - | - |
| *C.latius* | 0 | 0.07 | 0.14 | 0.48 | 0.29 | 98.89 | 17.90 | 0.00 | 1.25 |
| *E.vacha* | 0 | 0.08 | 0.14 | 0.48 | 0.29 | 99.17 | 41.00 | 0.00 | 3.28 |
| *D.devario* | 0 | 0.19 | 0.14 | 0.48 | 0.28 | 99.45 | 30.43 | 0.00 | 5.78 |
| *L.boga* | 0 | 0.03 | 0.11 | 0.48 | 0.23 | 99.68 | 33.91 | 0.00 | 1.02 |
| *P.guganio* | 0 | 0.01 | .09 | 0.48 | 0.18 | 99.86 | - | - | - |
| *L.angra* | 0 | 0 | .07 | 0.48 | 0.14 | 100 | - | - | - |
| **Total** | **1315.2** | **690** | | | | | | **31918.08** | **16430.34** |

Figure 2.8 Average abundance of species from modified and pristine floodplain/beel sites in the NE region where hydrological control is only partial. Species are arranged from top to bottom in descending order of their $\bar{\_}_i$/SD $\bar{\_}_i$ ratio. Only those species contributing to 75% of the cumulative average dissimilarity (column 7 in Table 2.6) are shown.

Table 2.7 Standardised fishing intensity for floodplain/beel habitat inside and outside

FCDI schemes in the NE and NW regions. NA - not available.

| | | Annual fishing intensity (std gear hrs $ha^{-1}$) | |
|---|---|---|---|
| Region | FCDI Scheme | Inside | Outside |
| NE | MIP | 51.4 | 35.0 |
| | SHP | 19.8 | 6.2 |
| NW | PIRDP | 3694.0 | 1923.0 |
| | PB | NA | NA |

## 2.5 Discussion

Informal evidence (Figure 2.5a) indicated that, with the exception of main and secondary river, species assemblages in Bangladesh appear to differ according to both habitat type and geographical location (region). Formal evidence for this pattern was shown by floodplain/beel and secondary river habitat in the NC, NE and NW regions (Figure 2.5b and Table 2.4). Interestingly, the vertical separation of sites within Figure 2.5, indicating assemblage dissimilarities across regions, closely matches the actual latitudinal separation of these regions within Bangladesh. The fact that the NC and NW regions are located within similar latitudes in the country would seem to explain their lack of vertical separation in the ordinations. Differences in species assemblages among habitats is expected on the grounds that different habitat types will possess different morphological, chemical and physical characteristics. Only certain species will have evolved adaptations necessary for life in these conditions. Different habitat types may also offer different numbers of niches based largely on the complexity and dynamic nature of the habitat.

Similar differences in assemblages linked with habitat type have been identified by Barrrella and Petere (1994) in the Jacare Pepira River, Brazil, where distinct assemblages were identified for four different habitat types: floodplain, rapids, headstreams and mid-river tributaries. Explanations for differences in species assemblages across latitude, particularly in relation to their diversity have been discussed by Lowe-McConnell (1987), Wootton (1990) and McDowall (1994). These are based largely upon the idea that abiotic conditions are less predictable at higher latitudes and hence fewer species have evolved the necessary adaptations for life in these conditions. Extinction probability is also likely to be higher within these unpredictable environments. Differences in latitude between the geographic regions in Bangladesh are, however, relatively small. Perhaps a more plausible explanation for the observed differences may lie with the close orientation of the main river system along the north-south line. Water flows downstream from its sources to the north to eventually join the Bay of Bengal to the south. According to the river continuum concept (Vannote *et al*, 1980) or the established relationships between stream order and species richness (Lotrich 1973; Horwitz, 1978; Welcomme, 1985; Wootton, 1990) or the abiotic-biotic continuum

concept of Zalewski and Naiman (1985), species assemblages would indeed be expected to vary with latitude in this case.

Because of these naturally occurring dissimilarities, valid comparisons of species assemblages caught at modified and pristine sites were achieved by maintaining the stratification of the data by both habitat and region (Figure 2.6). However, due to the unbalanced sampling design of FAP17, six of the twelve possible habitat/region combination (main river habitat is not modified in Bangladesh), comparisons could not be made because of the absence of replicate sites from modified or pristine locations. Moreover, only two of the remaining six combinations had sufficient numbers of replicates to test the null hypothesis at the 5% level.

The absence of any dissimilarity in the species assemblages caught from floodplain/beel habitat at modified and pristine sites in the NC may be explained by the fact that the construction of the FCDI scheme in this region (CPP) is incomplete (Table 2.1) and has no influence on the flooding patterns (FAP 17, 1995b). Flooding occurs naturally via the Lohajang River to the south-east of the scheme although a series of sluice gates within the embankment impairs the flow of floodwater in canals connected to the Pungli and Northern Dhaleswari rivers to the north and west of the scheme. This impaired flow would seem to explain the informal evidence for assemblage dissimilarity at modified and pristine canal sites.

Floodplain/beel habitat in the NE region was one of the two habitat/region combinations which exhibited statistically significant differences in the assemblages caught at the two site conditions. Modified sites were located in two different schemes; the MIP and the SHP, both of which offer only partial hydraulic regulation due to breached and submersible embankments, respectively. It is interesting to note that the two modified sites lying outside the closely clustered group at the top of the ordination, are located in the SHP. These two sites showed less dissimilarity in their species assemblages with pristine sites compared to the other three. In both cases, partial regulation would appear to have an impact on species assemblages though this impact appears less pronounced in the case of submersible than non-submersible, breached embankments.

Floodplain/beel habitat in the NW region also exhibited statistically significant differences in species assemblages caught at the two site conditions. The modified sites are located in two schemes; the PB and the PIRDP, both of which exhibit full flood control and have no submersible or breached embankments. The geographical position of sites within the NW region appears to explain their 'spread' within the ordination. The main group of sites (both modified and pristine) in the centre of the ordination are located within and around the PIRDP scheme. The two 'outlying' sites, one modified, one pristine, seen in the bottom left and right of the ordination respectively, are associated with the PB scheme located approximately 50km north of the PIRDP scheme. This suggests that geographical location within a particular region may also influences species assemblages.

An *R* value of 0.42 and the pattern displayed in the ordination suggested that real differences in assemblages between the two site conditions may also exist for secondary river habitat in the NW. A greater number of pristine sites would be required to support this inference statistically.

For canal habitat in the SW region, the apparent similarity of one of the modified sites to the group of pristine sites is likely to have prevented the rejection of the null hypothesis at the maximum attainable significance level (P = 6.6%). This modified site is located within the CFP, a scheme providing only partial flood control as a result of breached embankments. Conversely, the modified site furthest from, and therefore most dissimilar to, the pristine sites in the ordination is located within the SBP which provides full hydraulic control.

In floodplain/beel habitat of the NW region, 25 species were absent or less abundant at modified sites compared to pristine. The majority of these species are large with an average adult size of 54 cm[4] , and many of them, including *C.garua, O.pabda* and *W.attu* are known to be piscivorous predators (Rahman, 1989; Kottelat *et al*, 1993). Species that

[4] All average sizes are calculated from data given in Rahman (1989)

were more abundant at modified sites compared to pristine (with the exception of *X.cancila*) were all very small with a mean adult size of 9cm. Similarly, for the floodplain/beel habitat in the NE region, the mean adult size of the species that were absent or less abundant at modified sites was also high (40 cm) compared to those that were more abundant at the modified sites (10 cm). The latter figure exclude *Hilsa ilisha* since its presence is believed to be erroneous (see below).

This pattern is indicative that assemblages at modified sites have suffered ecosystem overfishing or the fishing-up process described in Section 2.1. Indeed fishing intensity in floodplain beel habitat was shown to be significantly greater inside the FCDI schemes in these two regions compared to outside (Table 2.7).

Alternatively, recruitment of migratory species to inside floodplains may have been diminished or prevented altogether by the effects of FCDI embankments on migration routes. In the NW region, the majority of the 25 species which were absent or less abundant at the modified compared to pristine sites are Silurid catfish (*P.atherinoides, C.garua, M.bleekeri, A.coila, S.silondia, H.fossilis, G.youssoufi, O.pabda, M.vittatus*, and *W.attu*). Many of the genus within this order are known to make long distance and lateral migrations within the river-floodplain system (Lowe-McConnell, 1975, 1987). This includes *H.fossilis*, which would be regarded as a 'blackfish' because of its physiological and morphological adaptions for surviving extreme environmental conditions, but is known to undertake lateral migrations (Welcomme, 1985). Seven of the species belong to the *Cirrhinus*, *Labeo* and *Catla* genus of the cyprinid order which are also known to exhibit significant migratory behaviour within or between biotopes. *L.bata, L.calbasu* and *L.guntea*, *C.mrigala* and *C.reba* are likely to be long-distance migrants, which swim upstream to spawn on open substrate. *Catla catla* and *L.rohita* on the other hand, generally exhibit only local lateral migrations. (Lowe-McConnell, 1975 as cited by Welcomme, 1979 Table 3.11). *Hilsha ilsha* , *G. chapra* and *C.soborna* are all clupeids. This family of fish have soft fin rays, particularly suited for swimming in open water and renowned for their migratory behaviour (Lowe-McConnell, 1987). *Hilsha ilisha* is anadromous, migrating upriver to spawn on open substrate (Welcomme, 1985). *Gudusia chapra* and *C.soborna* are likely to behave similarly. The loach, *N.botia*,

the goby *G.giurus* and the mullet *R.corsula* are mostly found in rivers and streams (Rahman, 1989). Riverine species are known to be very mobile, often moving long distances up and downstream and migrate laterally in response to flooding (Lowe-McConnell, 1987). The remaining species may also be migratory white or greyfish species, though evidence presented by MRAG (1997) suggests that *Puntius sophore* may be a beel-resident or blackfish species.

The five species of fish which were more abundant at the modified sites compared to the pristine are more characteristic of the less migratory resident black or grey fish categories, with traits resembling *r*-selected species. *Mastacembelis pancalus* secretes as protective layer of slime over its gills to promote oxygen diffusion in aerial conditions and the remaining species, *S.phulo, C.nama* and *C.ranga*, with the exception of *X.cancila* are all very small in size (mean size = 9 cm). Species of small adult size are able to mature rapidly, possibly within one year, sustaining populations upon the floodplain throughout the year, thereby removing the need for migrations across biotope boundaries. The *chanda* genus in particular is so small (5-8 cm) that it is unlikely to be capable of any significant migrations.

With the exception of a few cases, the pattern observed in the NE region was remarkably similar. Almost half of the species that were absent or less abundant at the modified sites compared to the pristine also belong to the siluroid order: *M.bleekeri, W.attu, N.notopterus, M.tengra, M.aor, M.cavasius, C.chandramara* and *C.garua*. Three clupeids: *G.chapra, P. ditchela and C.soborna* were also less abundant at modified sites as were the loach *S.gongota* and the same goby *G.giurus.*

Correspondingly, the majority of species that were more abundant at the modified sites compared to the pristine were also generally small, several belonging to the same genus: *Xenentodon, Chanda*, and *Salmostoma*. This group also contained three species of the genus *Colisa*; also conspicuous members of the 'blackfish' group. This genus possesses morphological adaptations for surviving low dissolved oxygen concentrations in the form of labyrinthiform suprabranchial accessory respiratory organs (Rahman, 1989).

Species belonging to the same genera including *Puntius*, *Salmostoma* and *Mastacembelus* were, however, often more abundant in modified than pristine floodplains and *vice versa*. These genera may belong to the 'greyfish' category and thus may not respond in a predictable way to the loss or reduced accessibility of migration routes. Alternatively, species within these genera may simply exhibit different migratory responses. Different migratory responses within a genus have been reported for *Labeo and Barbus* in Lake Victoria, and *Alestes* in the Niger (Daget, 1952; Whitehead, 1959 and Welcomme, 1969 as cited by Welcomme, 1985). Differential migratory responses between forms of the same species have also been reported by Wootton (1990). Size is likely to be an important factor in determining the potential for migration, particularly within swift currents in the main channel (McDowall, 1994). For the *Salmostoma* genus the smaller of the two (*S.phulo*) was more abundant at modified sites and is generally found only in streams, floodplains and beels, whereas the larger species ( *S.bacaila*) is also found in main rivers (Rahman, 1989). Similarly, the larger *M.armatus* is more abundant at pristine locations whereas the smaller *M.pancalus* is more abundant at modified sites.

Levees and embankments have been shown to act as obstacles to fish migrations in a number of other river systems, particularly, (dis)tributaries of the Mississippi, which have been extensively modified by levees. In the Illinois river, the abundance of species dependent upon the floodplain for spawning habitat including pike (*Esox lucius*), large-mouth bass (*Micropterus salmoides*) and yellow perch (*Perca flavescens*) have diminished as a result of levee construction (Bryan & Sabins, 1978 as cited by Welcomme, 1985). Other members of the centrachids (sunfishes and bass) as well as ictalurids (bullhead catfish) have also declined in abundance in leveed sections of the Atchafayia river (Fremling *et al*, 1989). Species of small cyprinids *Hybognathus argyritis* and *Hybognathus placitus* which exploit silty backwaters to feed on organically rich mud and ooze in the Missouri river have also declined in abundance, presumably due to loss of floodplain habitat or because they are obstructed from migrating onto the floodplain (Pflieger and Grace, 1987). In eastern Europe, Bacalbasa-Dobrovici (1985;1989) postulate that levees constructed on the banks of the Danube have excluded and reduced the abundance of a number of phytophilic and semi-migratory species such as common carp (*Cyprinus carpio*), pike (*Leucius idus*) and sheat fish, although catch

rates remained relatively constant. Further examples are given by Welcomme, (1985) and synthesised more generally by Welcomme *et al* (1989). Curiously, Regier *et al* (1989) suggest that levees and embankments suppress blackfish species (in addition to whitefish) despite defining their wet and dry season habitat as being floodplain.

In the NW region the abundance of small, low value, 'black' and 'greyfish' was significantly greater in modified sites compared to pristine. This apparent compensation might be due the absence or reduced abundance of large piscivorous predator species which would otherwise prey on these species. This type of response has been observed by a number of workers. For example, Tonn and Paskowski (1986) found that mudminnow (*Ubra limi*) densities increased significantly following severe winterkills of adult yellow perch (*Perca flavescens*) in lake habitat in North Wisconsin, USA. Caley (1993) periodically removed predators from artificial coral reefs which lead to increases in species richness and total abundance of resident non-piscivorous fishes. Both Caley (1993) and Zaret (1979) concluded that predators play an important role in structuring fish communities. Bayley and Petrere (1989 p387) exemplify the influence of predation on the abundance of prey species, in the Amazon system, Brazil, reporting that "...at least 75% of the production of fish and decapods up to 24 cm long in the varzea (floodplain) was consumed by piscivores". Campbell (1979) reviews the literature on predation in rivers and cites several examples where substantial reductions in predator population abundance has led to increases in the abundance of prey populations.

The unit value of the assemblages at the modified sites is up to 25% lower than pristine sites. However, a study by Thilsted & Hassan (1996) on the nutritional importance of small indigenous fish in Bangladesh, concluded that small species such *S.phulo, Chanda* and *Puntius* species and prawn species, which have been shown to dominate assemblages inside FCDI scheme, have a higher nutritional value than larger, the more valuable, highly prized species such as the carps *Labeo rohita* and *Hypopthalmichthys molitrix*. Although protein and fat content are similar between the two groups, small fish provide more vitamins and minerals, particularly calcium and vitamin A, because they are eaten

whole, including bones and organs. Small fish also have a lower unit value and are therefore more affordable.

Data intensive and computationally demanding analysis of this type begs the questions: "Could more simple techniques such as univariate methods or the use of more easily collected data such as presence/absence, detect the same impacts?" Clearly the answers to these questions have important implications for future survey designs and assessments of this type. To answer these questions the same null hypothesis: 'there are no differences in species assemblages caught at modified and pristine sites', was re-examined for the floodplain/beel habitat in the NW and NE regions in two ways. Firstly, with commonly applied univariate diversity indices: the number of species in the sample (*N)* and species richness *(S)* applied to presence/absence data and the Shannon-Wiener Diversity index *(H*') applied to the CPUE data (See Wootton (1990) or Clarke and Warwick (1994) for further details). The Student's *t*-test with pooled variance[5] was used to test for significant differences in the mean values of each index. The second approach was based upon multivariate MDS and ANOSIM methods applied to presence/absence data.

The means and 95% confidence intervals of each diversity index for both habitat/region combinations are shown in Figure 2.9. Examination of three graphs for the NE region indicate that assemblage diversity is marginally higher at the modified sites compared to

[5]The test is based upon the assumption of constant variance (Zar, 1984)

Figure 2.9 Mean and 95% confidence intervals for the number of species (*N*), species richness (*S*) and Shannon-Wiener diversity index (*H*') at the two site conditions for floodplain/beel habitat in the NE and NW regions.

Figure 2.10 MDS Ordinations for floodplain/beel habitat in the NW and NE regions based upon presence/absence data. Open circles denote pristine sites, solid denote modified sites (stress = 0.04, 0.01).

the pristine. However, none of the indices rejected the null hypothesis at the 5% level (P = 0.74; P = 0.45; P = 0.97). For the NW region, the null hypothesis was rejected for *N* (P = 0.01) and S (P = 0.01*),* but not for H' (P = 0.14*).*

The MDS ordinations from the multivariate analysis based upon presence/absence data are displayed in Figure 2.10. The ordination for the NW region shows unequivocal dissimilarity between the two site conditions. The ANOSIM test also rejected the null hypothesis at the 1.2% level (the maximum attainable significance level). The pattern displayed in the ordination for the NE region shows little dissimilarity between the site conditions; eight of the nine sites are overlapping. Despite a significance level of 5.6%, the dissimilarity between the two groups of sites appears dependent upon the single

pristine site located at the bottom of the ordination. For this reason it would be prudent to accept the null hypothesis.

In both regions, the Shannon-Wiener, the most commonly used diversity index, Clarke and Warwick (1994), was insensitive to the assemblages dissimilarities between site conditions. The number of species *N* and species richness *S* were equally insensitive to the dissimilarities present in the NE region. Only for the NW region, where there was a very significant difference (40%) in the mean number of species present at the two site conditions, did these two indices reject the null hypothesis. The results from the multivariate analysis applied to the presence/absence data revealed similar insensitivity to the perhaps subtle dissimilarities present in the NE region based mainly upon differences in species abundance as opposed to species absences.

In addition to the apparent insensitivity of these more simple approaches, they are inherently unable to identify or elicit detailed information about species responsible for assemblage dissimilarity between site groups or conditions. As was demonstrated in this analysis, this information is extremely valuable for providing explanatory hypotheses for the observed patterns, and to highlight the broader impact of changes to species assemblages.

## 2.6 Chapter Summary

- Species assemblages in Bangladesh exhibit dissimilarities between geographical region and habitat type.

- Because of poor sampling design by FAP17, only 2 of the 12 habitat/region combinations contained sufficient numbers of replicates in each site condition to test for differences between assemblages at the 5% level. This highlights the need for balanced sampling design with sufficient numbers of replicates for studies of this type.

- Assemblages caught from hydrologically modified and pristine floodplain/beel

habitat in the NW and NE regions were found to be significantly different ($P < 0.05$).

- Because of the close relationship between the three main ecological categories of fish and their positions along the *r/K* spectrum (Section 2.1), it is largely uncertain whether the observed differences are due to ecosystem overfishing or simply that the FCDI schemes act as obstacles to migrations and movement and thereby exclude, and reduce the abundance of large, migratory, high value 'whitefish' species including the highly prized Indian major carp species, in favour of small, low value, resident, 'black' and 'grey' fish species.

- If the latter is the case, FCDI schemes in Bangladesh do not exclude all migratory species, rather they tend to simply reduce their abundance. This implies that sluice gates and other 'regulators' allow some access between the main biotopes.

- Environmental stress other than exploitation by man (eg pollution) can also bring about similar responses, and hence their influence cannot be dismissed as being contributory or even responsible. This is exemplified by Natarajan (1989) who reports similar declines in the populations of 'whitefish' species (Indian major carps and *Hilsa ilisha*) in the Ganges in response to heavy exploitation and pollution. Similarly, catch rates were sustained by increases in the abundance of small cyprinids and air-breathing species (Welcomme *et al*, 1989). Backiel and Penczak (1989) also found that pollution in the Vistula River resulted in the decline of large, 'active' species, though catches of non-migratory species remained constant. Indeed, the difficulty in assigning such responses to specific stresses in large rivers is well recognised. Multiple stresses may be acting simultaneously and many "...mimic each other in their effects" (Welcomme *et al,* 1989).

- The unit value (TK/kg) of the assemblages was 25% lower in fully functioning schemes and 8% lower in partially functioning schemes. However, the nutritional value of the assemblages at modified sites, may be higher because

small species are eaten whole including calcium, vitamin and mineral rich bones and organs. Small species are also less expensive and therefore more affordable by the rural poor.

- Univariate methods or multivariate methods employing simple presence/absence data were found to be less sensitive to assemblage dissimilarity than multivariate methods applied to hard-won abundance data. The former methods are also unable to elicit potentially valuable information upon the abundance of species responsible for the observed dissimilarities.