The Coastal Habitats, Species Composition, Richness, and Temporal Variation of Haplochromine Cichlids in an African Great Lake: implications for biodiversity conservation

By

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A Thesis
Submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements
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Center for Earth Observation Science
Department of Environment and Geography
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Abstract

Freshwater parks and fisheries management zones in Lake Malawi are needed immediately but deficiencies in the underlying science prevents their design. In this dissertation I develop an empirical framework to enable aquatic conservation planning to proceed at the lake wide scale while taxonomic and species level ecology information remains incomplete. I investigate the effect of habitat discontinuities on the distribution of species to support the development of a habitat map for the entire lake that can infer the distribution of the main haplochromine cichlid assemblages. To better understand the ecology of the haplochromine species, I first examine how space, time, and environment (depth, substratum, temperature, total suspended solids) interact to influence the composition of haplochromine cichlids in rock, sand, and mud habitats in the southern basin of Lake Malawi. I studied 23 sites (0 – 125 m) using large samples collected biweekly or monthly for up to one year using SCUBA, seine nets, and benthic trawling. To better understand the richness of the assemblages I also studied the form of species accumulation and the temporal variation of the samples.

Complete survey of the coastal zone reveals the tectonic framework of the Malawi rift controls the distribution, slope, and scale of coastal habitat at regional and local scales. Rock or sand and vegetated shores alternate at up to 110 km spacing and reflect the dip polarity of half graben units that form the rift. Border faults form rock coasts whereas the shoaling margin of half grabens are sandy. Geomorphology is a good indicator of coastal zone composition; the length of coastal habitat for rock, sand, and sand/vegetation are significantly different among the geomorphologic settings bounding the lake. In the littoral zone, the depth of the rock/sand boundary also varies according to the geomorphology but rarely extends deeper than 40 m. The sand/mud boundary is abrupt and occurs at depths greater than 65 m, except where fluvial sediments are deposited and constrict the littoral.

The haplochromine assemblages can be reduced to three groups (i.e. rock, shallow water sand, deep water mud), not two as previously thought. The regional species composition of the rock dwelling mbuna on the mainland coast mimics the alternating pattern of rocky border faults; endemism and tectonics appear to be linked. The species composition of the deep water haplochromine assemblage over mud is quite different from the adjacent species in shallow water (i.e. sand). The rock, sand (shallow water), and mud (deep water) assemblages exhibit two forms of ecological attributes that reduce to smooth and rough bottom assemblage types. The mbuna and non-mbuna on rock islands have asymptotic species accumulation curves, few rare species, and low temporal variation in species count statistics. The haplochromines inhabiting smooth bottoms have non-asymptotic curves, many rare species in water less than 30 m depth, a temporal variation of abundance that is 1.7 – 2.0 x the magnitude of the rock dwelling mbuna, and a changing species composition over time. Accordingly, space (i.e. distance) is a strong descriptor of changes in species composition for the mbuna. The importance of space is relatively low on the smooth bottomed habitats, and is least for the fishes in deep water over mud. The geographic range of the species pool on rock islands appears small and the fishes are sedentary; the concept of site richness applies readily to this group. The geographic range of the species pool for fishes of the smooth bottomed habitats appears much larger; this group is literally a moving and numerically variable target for conservation.

Results suggest that parks planning and fisheries management zones should be allocated regionally according to the distribution of rock, sand, and mud (i.e. deep water) within each of the 100 km long half graben units that comprise the rift. The relative size of the management units appear to ordinate as small, moderate, and large for the mbuna, shallow sandy (0 – 50 m), and deep mud (50 – 125 m) haplochromine assemblages. Richness of these assemblages cannot be compared directly due in part to a combination of large numbers of rare and mobile species in the sandy shallows that equates to incomplete sampling. The perimeter of parks for the rock dwelling species can mimic local distribution of rock, but the sand and mud habitats are extensive in size and the limited knowledge of these fish prevents an absolute size recommendation.

Acknowledgements

I extend sincere appreciation to Dr. David G. Barber, my advisor, who has made clear to me science as a process, and that creating great opportunities is key to develop good scientists. I thank Dr. R. E. Hecky for a making a fateful comment back in 1990, that I actually took as a joke, in that we might one-day travel to Africa and that I could experience the cichlids in their natural habitat. I thank Dr. W. G. Franzin for providing a habitat mapping task for my 4th year cartography class, which ended up being a turning point in my direction. Each of my committee members has created opportunities that shaped my way of thinking and for that I am grateful.

This work depended on many people. In particular, I thank Dr. A.J. Ribbink, JLB Institute of Ichthyology, South Africa, for making the mbuna species identification. Without his help I would have failed. I thank Robert Sululu and Fabrice Duponchelle who were kind enough to incorporate my aspirations into the design of the sandy and offshore surveys and to make the data available. I also thank Greg McCullough, who helped in many ways. We were drifting on the lake when he made a comment that epitomized my African experience: after biting into a Mango, Greg looked out over the calm lake in the sun from underneath his hat and behind his sunglasses and said..."pretty tough to beat". He was right!

The members of the Lake Malawi biodiversity conservation project also helped: Dr. H. A. Bootsma, Capt. M. Day, Dr. J. Snoeks, M. Hanssens, A. B. Thompson, F. X. Mkanda, W. Taylor, R. Brook, Patricia Ramlal, Richard Kula, Mr. Banda, Geoffrey Wani, Alias, Mistone, Joeseph, and Leno. At the University of Manitoba: D. Mosscrop helped in many important ways and D. Walker provided a multivariate primer. Dr. Bill Last, Geological Sciences, facilitated the grain size analysis.

I thank the University of Manitoba for granting an MGF Fellowship. The radar data were provided with an ADRO research grant, through Dr. Barber. Finally, I thank the following funding agencies for recognizing the uniqueness of the system and the combined need for research, conservation, and management: World Bank, CIDA, SADC, GEF, ODA, and WWF. *Zikomo Qwamberrie!*

Dedication

I dedicate this volume to my endearing and eternally supportive wife, Cathy, who confidently carried our first unborn son while I was abroad during my final field experiment in Malawi, and realistically, ran our family smoothly ever since then, and without complaint. To my young sons Kevin and Kyle: you each could not make me more proud. Yes…Daddy's book (that doubles as a door stop!) is finished. This dedication is a reminder that each of you is first, everything else in life is second…and that is the most exciting notion of all!

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Chapter 1 Introduction

In this research I strive to develop a new scientific understanding of fish diversity in Lake Malawi that can direct the unattended needs of conservation planning. The vehicle for this insight is an empirical framework of linked interdisciplinary studies that combine physical geography, ecology, and biogeography. This penultimate objective is constrained by the fact that Lake Malawi is the ninth largest lake in the world, has an unrivalled species richness (Snoeks 2001) and taxonomy that is far from complete. Most of this diversity in found in the littoral zone (Ribbink et al. 1983) which, unlike the species poor pelagic region of the lake (Patterson and Kachinjika 1995), has received little systematic study.

The need for a conservation strategy is immediate and urgent. Study of Lake Malawi dates back more than a century, but most empirical evidence of the marvelous haplochromine cichlid (Teleostei: Cichlidae) diversity has arisen only recently (Ribbink et al. 1983, Konings 1996, Turner 1996). These studies show that rock and sand habitats have different species and distill the importance of the system as a unique but poorly understood laboratory of evolution. Rapid increases in deforestation in areas of the catchments in recent decades also has increased the input of terrestrial sediments into the lake (Kingdon et al. 1999, Mkanda 2002, Hecky et al. 2003). This has created concern for water quality and sedimentation of benthic fish habitat. The situation is clear: a lack of baseline data prevents a complete understanding of species diversity and precludes the ability to assess change.

The design of a conservation strategy for the entire lake cannot be based on rock and sand haplochromine species distributions because this information is far from complete. Physical habitat distributions could provide a way to infer species distributions, especially for the rock dwelling cichlids because allopatry (Kornfield and Smith 2000) and the controversial hypothesis of recent drops in lake level (Owen et al. 1990) are thought to have been important in their adaptive radiation. However, the habitat distributions of the lake remain unknown, as is the understanding of how the form of the Rift Valley controls habitat availability at different water levels. The poor understanding of the sand dwelling haplochromines limits our ability to compare mechanisms for speciation between the rock and sand assemblages, or to determine if the changes in species composition over space (i.e. distance) is similar. Would conservation areas all be the same size, or could the ecology of the assemblages suggest the relative size and relative importance for conservation? What is certain is that the end use of these two groups of cichlids is very different. Interest in the colorful rock dwelling cichlids is mainly by the international community for science and tourism; freshwater parks would be envisaged for this group. The less colorful and more easily exploited fishes inhabiting sand are almost unstudied but form a critical source of protein for the people of the riparian nations. This group of fishes would be the target of fisheries management.

In the light of perceived environmental change and fisheries exploitation I contend effective conservation and management cannot wait for complete taxonomic survey and ecological certainty. An indirect approach is needed that provides a short-term basis to both understand the habitat variables that influence species composition and to use them to partition this vast system into more tractable pieces. Do the discontinuities of the readily observed coastal and littoral habitats create abrupt changes in species composition? Do ephemeral variables such as water temperature or total suspended sediments effect seasonal changes in composition? If not, the persistent habitat boundaries, such as the rock/sand boundary, could double as boundaries of parks or management units. In this manner, the zoning of the lake into conservation and management districts is not arbitrary but is designed in harmony with the physical framework of the lake that has been, at least in part, responsible for the diversity we observe today.

The research design of this dissertation is hierarchical with data represented at local (0.050 km – 37 km), region (100 km), and system scales (680 km), with unequal representation of physical and biological sampling over space and time. Physical data span all three spatial scales to meet the need for lake wide observations and to couple with the biological data that can be collected reasonably at the site and regional scale. The habitat observations are collected during short periods of time (1 – 14 days), whereas the biological data are temporal samples collected at either biweekly or monthly intervals for up to one year.

This dissertation is a part of an international effort to provide baseline information on this unique ecosystem. The Lake Malawi Biodiversity Conservation Project (LMBCP) arose at the request of the riparian countries of Malawi, Tanzania, and Mozambique, to the Global Ecological Facility (GEF) to address the concern for changes within the drainage basin, a limited knowledge of the lake and its diversity, and a need develop a management plan for the lake. The Center for Earth Observation Science provided four graduate studies to the LMBCP that approached the problem from a physical process perspective that coupled the aquatic and terrestrial environments[1]. This dissertation links to these studies by investigating the spatial pattern of physical habitat, including lakebed sediments, and the association of haplochromine fishes to physical habitat.

1.1 Thesis objectives

The main goal of this dissertation is to assess if the general distribution of species can be inferred at the lake wide scale:

> *Primary Goal: "Can physical habitat distributions observed at local scales be used as a proxy to infer changes in haplochromine species composition and provide a template for conservation planning at the lake wide scale?"*

To assess this question methods must be developed to acquire the extensive coastal and littoral data, including a site considered to be evidence of a low lake stand. To fully interpret the physical habitat distributions the tectonic setting will also need to be considered.

It is my opinion that partitioning the lake into smaller conservation and management areas is needed for political, ecological, and practical reasons. How would the size of any conservation areas be decided? Which of the rock and sand assemblages has a higher richness? Two main corollary questions are therefore:

> *Secondary Goal: "Can the haplochromine species composition data suggest relative sizes of conservation areas and can the assemblages be ranked in terms of importance?"*

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[1] The other CEOS graduate level studies were cloud climatology (A. Pegado, Mozambique), terrestrial soil loss estimation (F. X. Mkanda, Malawi), lacustrine sediment plume dynamics (G. K. McCullough, Manitoba, pending).

Spatial and temporal sampling is important in a species rich system because repeated sampling of a structured series of sites more fully enumerates the richness, and also can provide an assessment of the effect of space and time on changes in species composition. If rock and sand assemblages ultimately have a similar richness the temporal variation during the sampling may provide additional insight to assess differences between assemblages.

My specific research questions, which derive directly from these main considerations, are:

1. *Can remote sensing be used to map the coastal zone of tropical lakes?*
2. *How does the Malawi Rift influence the horizontal distribution of coastal habitat discontinuities at regional and local scales? Can a site reported as a 120 m low lake stand less than 500 years ago be validated? Is the regional distribution of the rock habitat similar to the distribution of rock dwelling mbuna species composition? Does this information improve the understanding of allopatry in the lake?*
3. *Are habitat discontinuities present in the littoral zone as water depth increases? If so, does allochthonous sedimentation change this pattern at a site near a river mouth?*
4. *Do the habitat discontinuities evident in questions 2 and 3 influence species composition, and is there evidence to suggest that ephemeral changes in the environment cause seasonal shifts in the composition? Can the composition data suggest a relative size for conservation areas?*
5. *Can the fish data be ranked into ordinal classes based on species richness to infer priority for conservation? How many samples are required to sample sufficiently each of these assemblages? Is there information contained in the accrual of species or temporal variation that helps to illustrate differences between assemblages?*

In question (1) I examine the feasibility to use satellite remote sensing to classify the coastal zone of Lake Malawi. Due to the ubiquitous cloud cover and the limited width of the coastal zone I select and compare the ability of synthetic aperture radar (SAR) offered by the RADARSAT satellite to the familiar optical data provided by SPOT to discriminate and classify rock, sand, and vegetation. Using a case study from the southern basin of the lake, I first evaluate the effects of the RADARSAT system parameters (i.e. coherent fading, look direction, and incident angle on the magnitude of backscatter tone. This will assess the feasibility of classifying an image mosaic with a range in these parameters because they cannot be standardized at low latitudes. I then test the average backscatter response among the rock, sand, and vegetation classes to determine the statistical merit for use in discrimination and classification. To assess if SAR can be used to effectively discriminate and classify rock, sand, and vegetated coasts I use radar backscatter and geometric variables that can be readily obtained from the images and on-site measurements, and compare classification by these means to the classification of SPOT. Finally, I assess the merit of combining SAR + SPOT to evaluate an entirely remote approach for discrimination and classification that does not require site visits.

Question (2) investigates the distribution and scale of coastal habitat for all of Lake Malawi and will express the relationship of coastal habitat to the tectonic setting of the Malawi Rift. This is important not only to demonstrate the horizontal pattern of habitat around the entire lake, but because lake level variation is thought to have played a role in the adaptive radiation of the cichlids, an understanding of how the landform controls the expression of coastal habitat can also help to understand habitat composition of low lake levels in the past. Statistical analyses will show how the landform, coastal type, and slope are related and also to illustrate any differences in the scale of each habitat type by landform. The hypothesis of a low lake stand 120 m below present less than 500 years ago has spurred much controversy. I will study a site reported as evidence of a low lake stand to provide a critique of the surficial character and the historic and contemporary variables that may explain the feature. Finally, the regional pattern of rock habitats will be compared to published information describing the regional distribution of the rock dwelling mbuna. This last objective intends to link forcing and response between the tectonic framework of the basin and the habitat and species distributions. It also infers the main form of allopatry during recent time.

In question (3) I continue to examine the theme of habitat discontinuities started in question (2), but the focus shifts from the segmentation of the coastal zone in the horizontal sense to explore discontinuities that occur vertically in the littoral zone (i.e. as water depth increases). I place particular emphasis on the deep water habitat discontinuities for two main reasons: 1) the deep water setting is unstudied, 2) delineation of a deep water habitat boundary in the mainly sandy areas of the lake could be combined with the coastal habitat map of question 2. This could form a substratum template for the entire lake and provide a basis to assess if these boundaries influence species composition. To capture any deep water boundaries I employ digital sonar linked to global positioning systems and map depth and acoustic signatures of the substratum in 5 large areas of the southern basin. First, I will relate physical properties of the substratum to their acoustic signatures. This analysis will demonstrate the acoustic response for rock, sand/gravel, sand, and mud bottom types. Next, I explore the use of the acoustic signatures to discriminate and classify the lakebed. The benefit of these analyses will be to show the relative strengths and weaknesses of the approach. Finally, I implement the foregoing technology and classification method at all five sites including one site adjacent to a major source of terrestrial sediments. The purpose will be to compare the depth of mud deposition at the sedimented site to the other four sites that are unaffected by riverine inputs.

Question (4) investigates the potential influence of habitat discontinuities from questions (2) and (3) on the haplochromine species composition at local scales (24 – 39 km) sampled from rock, sand, and mud habitats in the southern basin. I explore relative influence of the effect of boundaries that are temporally invariant, such as the sand/mud boundary, but the influence of ephemeral variables is included because the study area shows seasonal variation in temperature and suspended solids. Multivariate and hierarchical analyses serve to assess simultaneously the relative roles of evolutionary (space, time) and environmental variables (depth, temperature, total suspended solids) that account for variation in the species data. An understanding of how species composition changes over space and time will provide valuable information that could describe the ecology of the assemblages and provide preliminary insight into the relative sizes of parks or fisheries management zones.

The last question (5) focuses on species richness to assess if the haplochromine assemblages of question 4 can be ranked to infer priority for conservation. To do this, I ask two main questions: 1) can richness of the assemblages be observed or estimated? This question will provide the information needed to assess if sampling can be considered complete for each assemblage. The total sum of richness is cumulative and does not convey the distribution of abundance among species. If the assemblages under study have similar levels of richness what other properties can be used to discern differences that could help conservation and management? The second question (2) exploits the information contained in the shape of the species accumulation over time and also investigates the temporal variation of the samples. The approach advocated here is that the usefulness of diversity or evenness indices in conservation is limited due to abstraction. Instead, a species accumulation curve may combine several properties of an assemblage into a single and easy to interpret graph and may facilitate comparing and contrasting the differences of different assemblages.

1.2 Thesis structure

This dissertation consists of eight chapters. In the first I have described the scientific context that rationalizes a need for this research, and the primary objectives and scope of the work. Chapter 2 provides a thorough background to the following chapters that address the 5 objectives in as many chapters. Research question 1 is presented in chapter 3 with the results being previously peer reviewed and published (See Cooley and Barber 2003). While the SAR results demonstrate clearly the effort was merited and successful, the approach requires precise ground positioning and requires extensive GPS surveys throughout the lake. Aerial surveys were employed subsequently to meet the needs of chapter 4. Question 2 appears in Chapter 4. Chapters 5, 6, and 7 present the results of research questions 3, 4 and 5. In Chapter 8, the thesis concludes with a summary of results and recommendations for future studies.

The body of evidence within this dissertation advances our understanding of biological diversity in Lake Malawi because this framework provides the initial basis for conceptual design of parks and fisheries management zones. The merit of demonstrating how species composition responds to discontinuities in physical habitat is realized when the more easily observed habitat distributions become the primary means for zoning the lake into conservation districts, and importantly, these boundaries also honor the evolutionary history. This helps the immediate needs of conservation planning by preempting the need to wait for complete taxonomic survey. This approach is not an alternative to a complete taxonomic survey. This work embodies a short-term proxy approach for initial site selection for conservation. Hopefully this improves the ability of future scientists to screen and allocate studies across this complex system.

Chapter 2 Background

2.1 Introduction

The Great lakes of the Eastern Rift Valley in Africa are marvelous centers of fish diversity with species richness that is unparalleled elsewhere in the world. Most of the richness of fish species derives from the family Cichlidae. Each of the three largest lakes, Victoria, Tanganyika, and Malawi, (Figure 2.1) has not less than 98% endemism of cichlid fishes (Ribbink 1983). Together, these lakes contain about 1, 715 cichlid species found only in these basins (Snoeks 2000). Lake Malawi, the second largest of these lakes, contains about 845 species (Snoeks 2000), or about half of the cichlid diversity found in the Rift Valley. Only about 300 have formal scientific names. Ninety percent of the known cichlid diversity in Lake Malawi is found in the shallow waters of the rocky coastal zone in less than 30 m of water (Ribbink 1983).

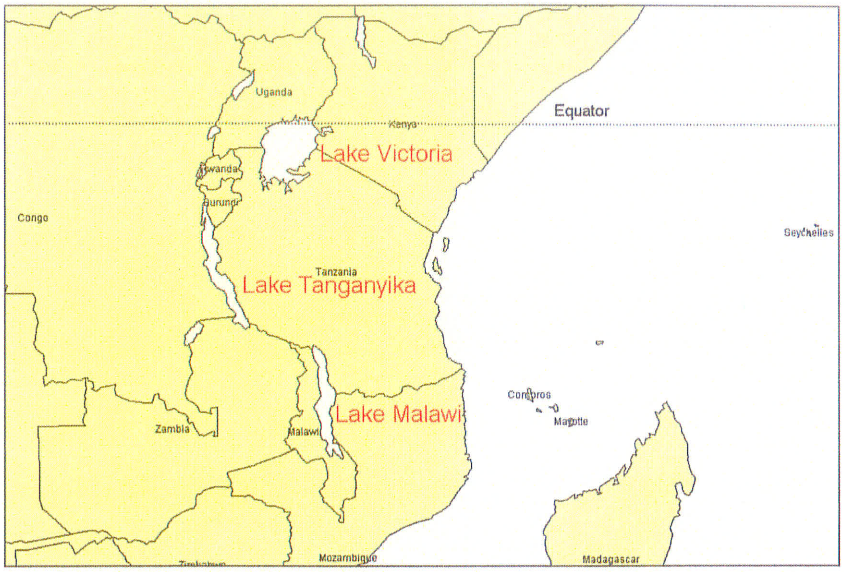

Figure 2.1. Lakes Victoria, Tanganyika, and Malawi in east Africa

The regional climate of Lake Malawi is dominated by the seasonal migration of the inter-tropical convergence zone (ITCZ), which results in a calm and rainy season from December to February, and a dry windy season from July to August (Johnson et al 1995). Historically, the oscillation of the ITCZ has resulted in changes in precipitation and evaporation in the region, and has provided a highly variable lake level with recent drops (c. 1500 – 1850) of up to 121 m (Owen et al. 1990). These lake level drops are thought to have produced complex and regional variations in sediment distribution and facies (Pilskaln and Johnson 1991). Owen at al. (1990) suggests that many of the fish taxa inhabiting the previously desiccated regions of the lake have evolved in less than 300 years, a controversial point in evolutionary biology.

Lake Malawi is 4 – 7 million years old and is located between 9.5 and 14.5 S in the southern branch of the East African Rift Valley. The Lake is 560 km long, 23 – 90 km wide, has a maximum depth of 700 m and is meromictic (Owen and Crossley 1989). The lake is anoxic below the chemocline at 250 m and is homothermal at 22.5 °C. The temperature of the water column above the thermocline varies annually from 24 – 27 °C (Eccles 1974, Gonfiantini et al. 1979). The mixed depth varies seasonally with the thermocline extending as deep as 125 m during the windy season (Gonfiantini et al. 1979, Duponchelle et al. 2000) but as shallow as 40 m at the onset of the rainy season in January (Duponchelle et al. 2000). The lake has a single outlet, the Shire River. Most of the 1.6 m variation in annual lake level results from evaporation.

The structural setting of the Lake Malawi rift can be divided into seven half graben units (Figure 2.2) that typically are 120 km x 40 km (Specht and Rosendahl 1989) with an alternating dip polarity along the north-south axis; each half graben unit is bounded on one side by a steeply dipping border fault, and the other side of the asymmetric cross section is the gradually shoaling margin. In other areas the lake is bounded by a variety of rift structures including, horsts and grabens, en echelon faults, tilt blocks, fault ramps and monoclines (Figure 2.3). The vertical displacement from the top of the Livingstonia Mountain range, 1.5 km above lake level, to the base of the sediment column adjacent to the border fault is greater than 5 km (Specht and Rosendahl 1989). On the east coast, one half graben to the south, 2.5 km of sediment has accumulated in the area of subsidence below the Usisya border fault. If the ages of the rift units can be correlated to the thickness of sedimentary deposits and the amount of vertical relief, then the age of the rift decreases from north to south (Specht and Rosendahl 1989). Crossley (1984) notes that the basin is deepest along single major border faults and is shallower below the other features.

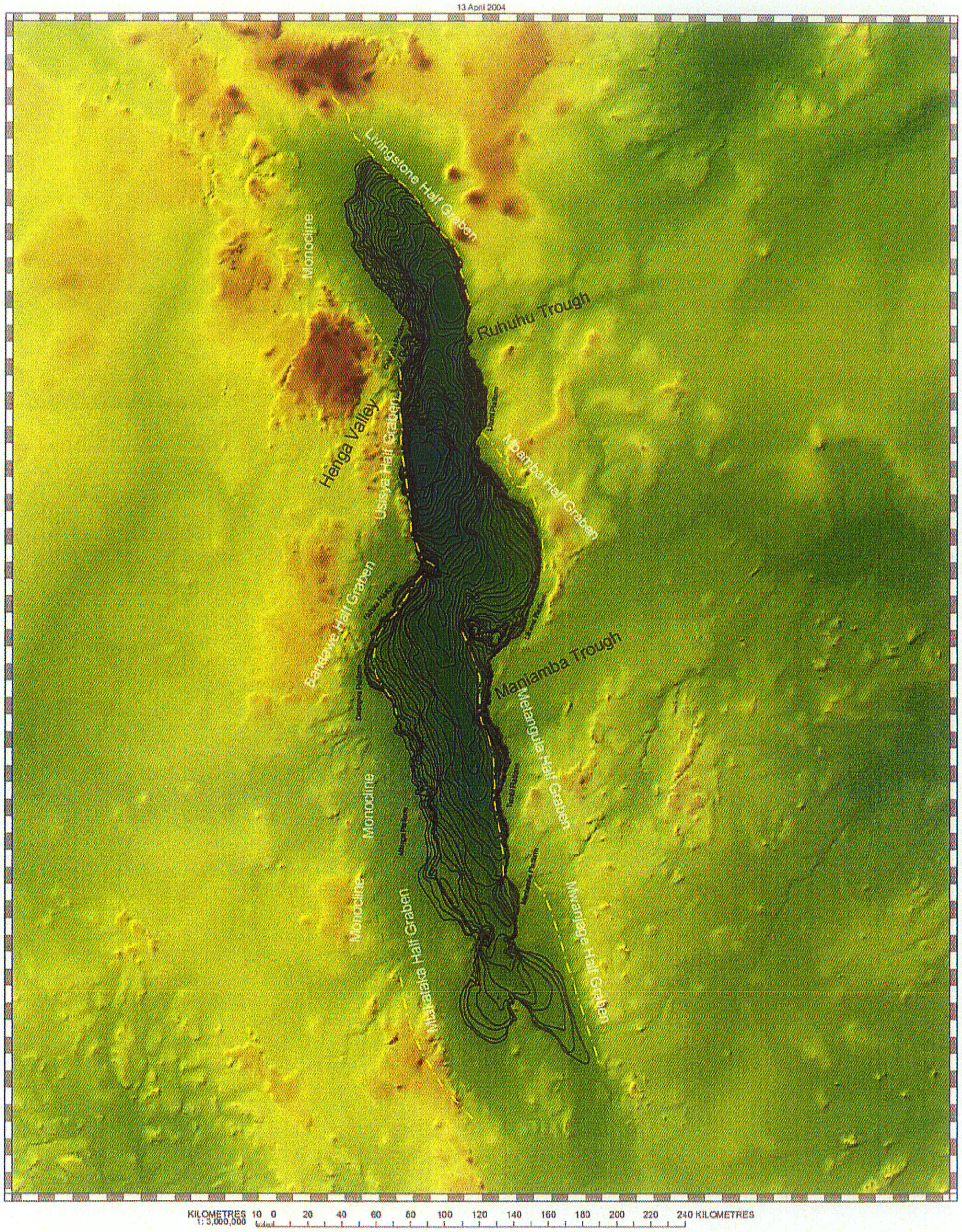

Figure 2.2. Tectonic framework of Lake Malawi. Half grabens (dot dash lines), monoclines (dashed lines) and regional elevation are shown. Adapted from: Cooley et al. 2003.

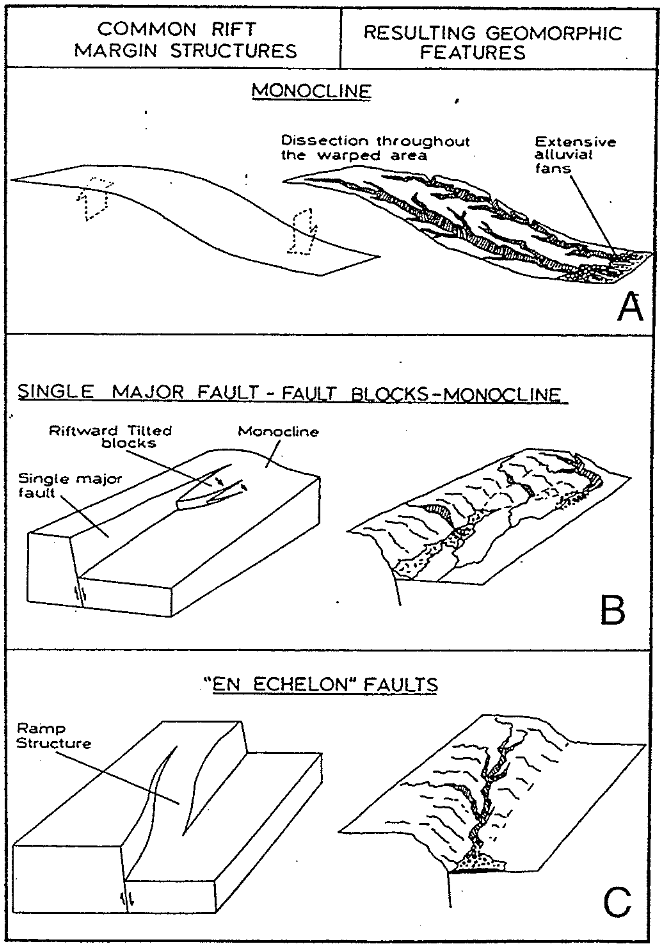

Figure 2.3. Common structures of the Malawi Rift and resulting drainage patterns. A) Monocline, B) major border fault, C) En Echelon Fault.

2.1.1 The Processes which Create and Maintain Fish Habitats in the African Great Lakes

The shallow water fishes of Lake Malawi exhibit a fine example of habitat selection (Ribbink 1983) and many fishes of Lake Malawi have a finely tuned relationship with their surroundings (Lewis et al. 1986).

2.1.1.1 What is Fish Habitat?

Fish habitat is derived from a suite of biotic and abiotic variables to which fish species have adapted. Definitions of fish habitat often encompass the variety of aquatic systems and their structural elements and conditions. For example, the Canadian Fisheries Act defines fish habitat as:

> *"Spawning grounds and nursery, rearing, food supply and migration areas on which fish depend directly or indirectly in order to carry out their life processes." (Canadian Fisheries Act, Section 34(1), Department of Fisheries and Oceans, 1986).*

This includes the quality of the waters and the "total surroundings" in which plants, invertebrates, and vertebrates, interact to produce fish life (Figure 2.4).

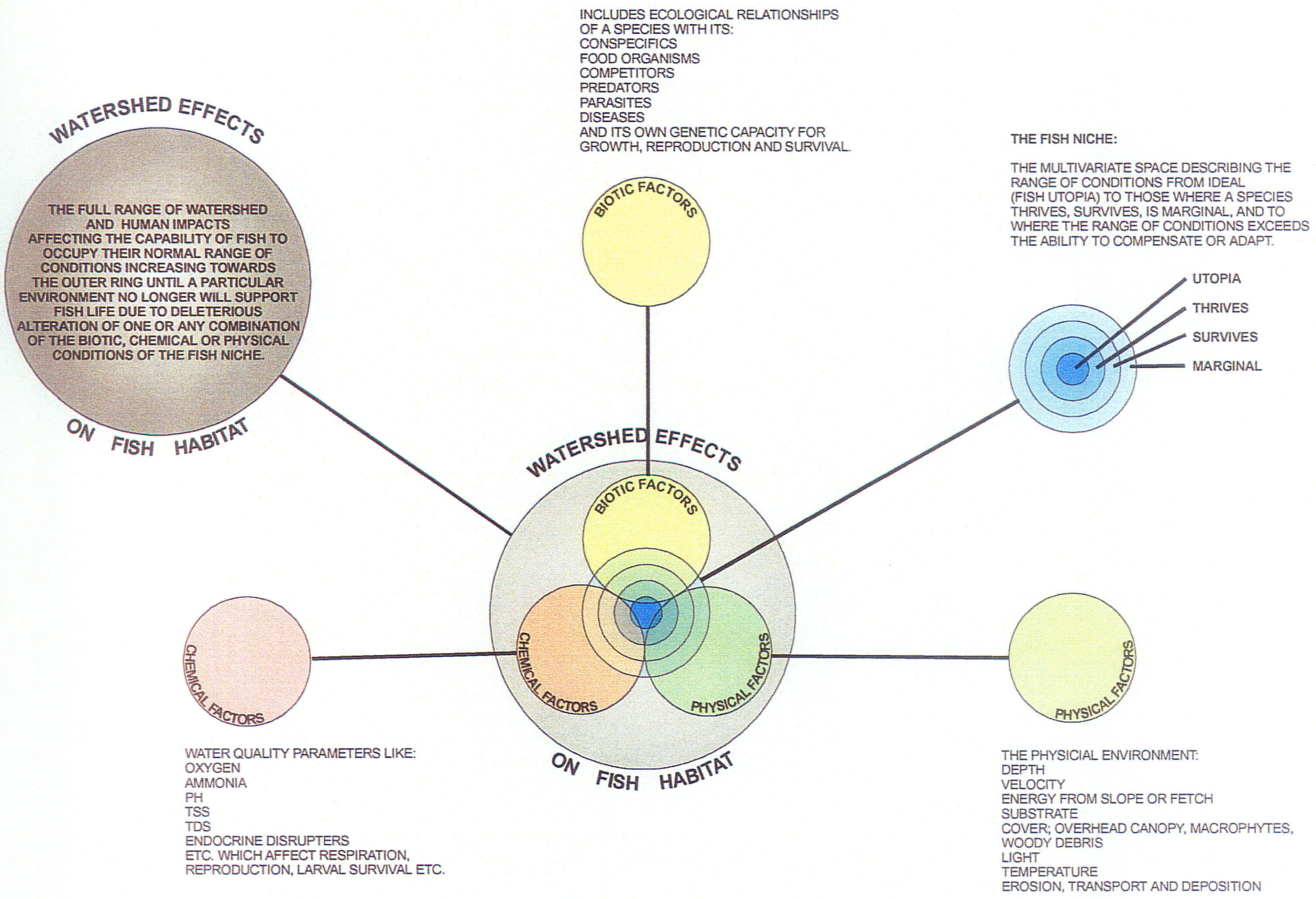

Figure 2.4. Biotic and abiotic factors of fish habitat. From: Franzin, Nelson, and Cooley, 2002.

2.1.1.2 *What is Physical Habitat?*

Physical habitat is a subset of abiotic fish habitat characteristics that includes earth materials, temperature, and water movements. Variation in the observed distribution and composition of these variables results from redistribution via the process of erosion, transport, and deposition. In this manner, physical habitat can be perceived as a variable of response that is affected by a series of forcing functions (Busch and Sly 1992).

2.1.1.3 *Habitat Forcing Variables:*

The substratum habitats of lakes are the complex products of geomorphology and the redistribution of the available materials by the hydrologic forces of water. Numerous variables combine to form and maintain coastal and littoral habitat distributions and these variables operate over a series of spatial and temporal scales.

2.1.1.3.1 *System, Regional, and Local Scale Factors*

The structure of the Malawi rift valley provides the main framework that sets the age, horizontal scale, range in elevation, and the nature of faulting in the earth's crust that determines the main distribution of landforms. Set within the regional climate, these small scale factors provide a feedback that establishes lake level regime and defines the physical extent of the aquatic habitat (i.e. lake size, shape, and depth).

The tectonic framework is important in determining the seasonality of river discharge by influencing drainage pattern, the form of deltas, the composition of fault blocks, and the main and local distribution of sediments in the lake basin (Crossley 1984, Owen and Crossley 1989, Johnson et al. 1995). In some areas of the basin, the elevation of rift structures interacts with the regional climate (in areas of high elevation) to create orographic precipitation that locally increases run off (A. Pegado, Mozambique, pers. com).

Cycles of land surface development and weathering within the present day drainage historically have been interrupted by faulting and volcanic activity. This is evidenced by a complex geomorphology and diverse suite of land surface features that range in age from within the Quaternary (less than 3 million years) to ancient features that date from the Jurassic-Early Cretaceous (180 – 130 million years ago) (Malawi 1986).

The geomorphology results from weathering and indicates a topographic sequence that represents mass wasting (Figure 2.5). The Scarp Zone is a steeply sloping landscape that forms the margins of the Rift Valley. Below, the Rift Valley floor in the area of Lake Malawi is called the Lakeshore Plains and includes both erosional and depositional landforms. Erosional relief includes low altitude dissected plains, piedmont zones and raised beach remnants with varying slopes. Depositional relief consists of nearly level land formed of fine alluvium. Rift scarps transport less clastic[2] material than the erosional areas of the depositional plains because erosional areas are much larger and offer a wider range in size of materials (Crossley 1984). The erosion, transport, and deposition due to weathering at the system scale sets up the regional pattern (i.e. availability) of earth materials.

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[2] Clastic refers to a fragmental mixture of rock derived from other preexisting rocks.

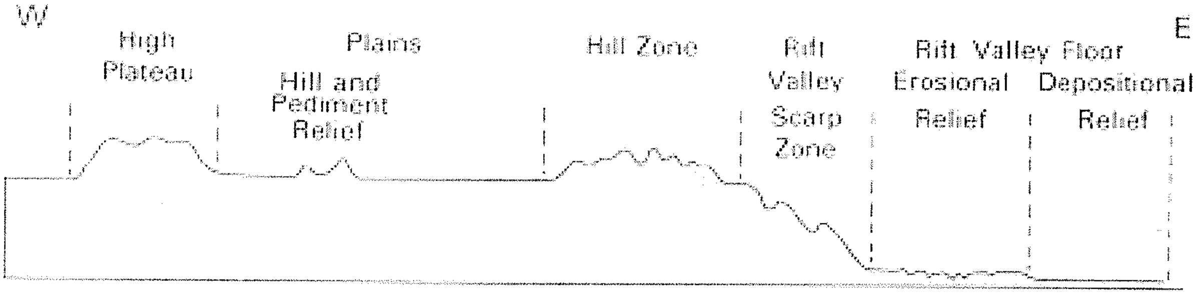

Figure 2.5. Topographic sequence according to the geomorphology classification of Malawi (1986). West and East compass directions are indicated with W and E, respectively.

At the regional scale of a half graben, lake level and geomorphology determine the slope and availability of materials available for erosion, transport, and deposition, and also sets the main geometry of the shoreline within the half graben. Wind, driven by regional climate transfers energy to the lake surface. The direction, magnitude, and periodicity of wind arising from within the half graben results in sub-maximal waves. The distribution of wave energy determines the maximum vertical scale of littoral habitat (when using the upper limit of mud as the definition of the littoral, see Bush and Sly 1992) in low slope areas.

Sediment focusing (Likens and Davis, 1975) describes material redistribution from the shallow zones of the lake into the offshore zone due to wave scour and slope, and results in the highly heterogeneous coastal and littoral substrata and homogenous offshore zones we observe. The erosion and transport of materials within the lake (i.e. of materials deposited previously by the noted small scale watershed processes), changes the bottom composition and slope of a local area. Variability in the composition and pattern of substrata at different sites can differ from the regional scale habitat composition and results from feedbacks among the system, regional, and local scale habitat forcing and response processes. I've not found literature to readily show this, so instead I draw from my data to show how the coastal zone responds to the local, regional, and system scale redistribution processes in Figure 2.6. The sections that follow describe the forcing variables in more detail.

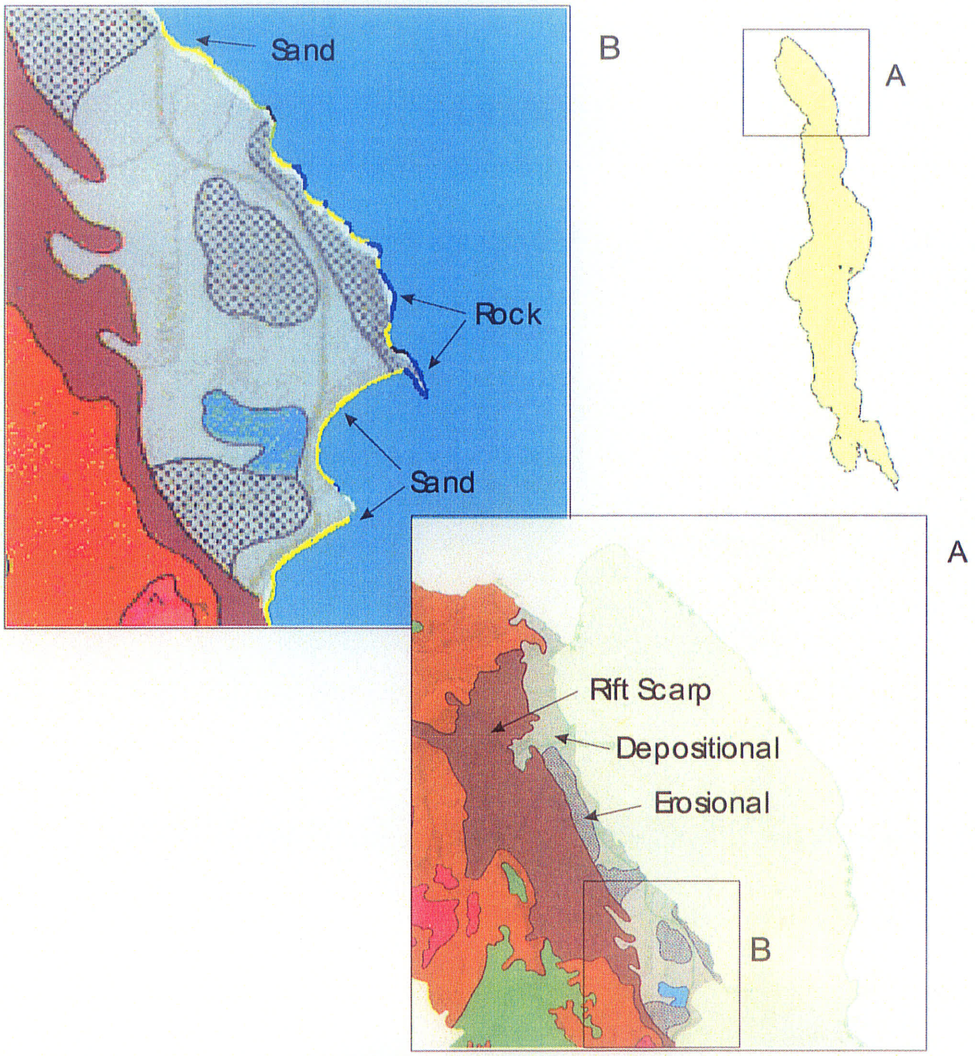

Figure 2.6. Coastal zone and hierarchical scales. "A": the linear Livingstone half graben. Variation in the geomorphology of inset "A" changes the coast. Locally, erosional zones "B" have different coastal shapes, scales, and frequent alternation.

2.1.1.3.1.1 Lacustrine Hydraulic Energy Factors

Erosion by surface waves occurs on the lakebed until the depth where the bed strength equals the erosive force (Luettich et al. 1990). Particles of different sizes, therefore, require different energy inputs for resuspension. Surface wave action in shallow water releases kinetic energy, both at the surface and at depth, which causes shoreline erosion (Reading 1986), sorts substratum materials by size (Busch and Sly 1992), and resuspends and deposits reworked materials into more energetically quiescent areas of the lake (Hakanson 1981).

Surface waves have been studied since the late 1800's (Hutchinson 1957). Surface waves are formed by the transfer of energy from the wind to the water. The shear stress created by the wind disrupts the surface tension of the water and sets the surface into oscillation. Initially, capillary waves develop. As the wind blows over a single ripple, an eddy of low atmospheric pressure is produced on the lee side. The effect of this eddy is to deflect the main wind momentarily upward. Beyond this disturbance the wind will fall with a downward component of momentum. This increases the atmospheric pressure on the side of the next wave exposed to the wind. Hence the water will be rising where the pressure is falling, and falling where the air pressure is rising. This causes the wave to grow in height as long as the wave velocity is less than that of the wind.

2.1.1.3.1.2 Surface Wave Development

A wave traveling across the water surface not only sets the surface into oscillation, but also causes oscillatory currents (Elliot 1986). Oscillatory water movements show a rotation of water molecules that attenuate with increasing depth below the wave (Figure 2.7). At the surface the diameter of the orbital path is equivalent to the height of the wave. The diameter of the orbital paths decreases with increasing depth until there is no motion, which is about one-half the wavelength (Hutchinson 1957).

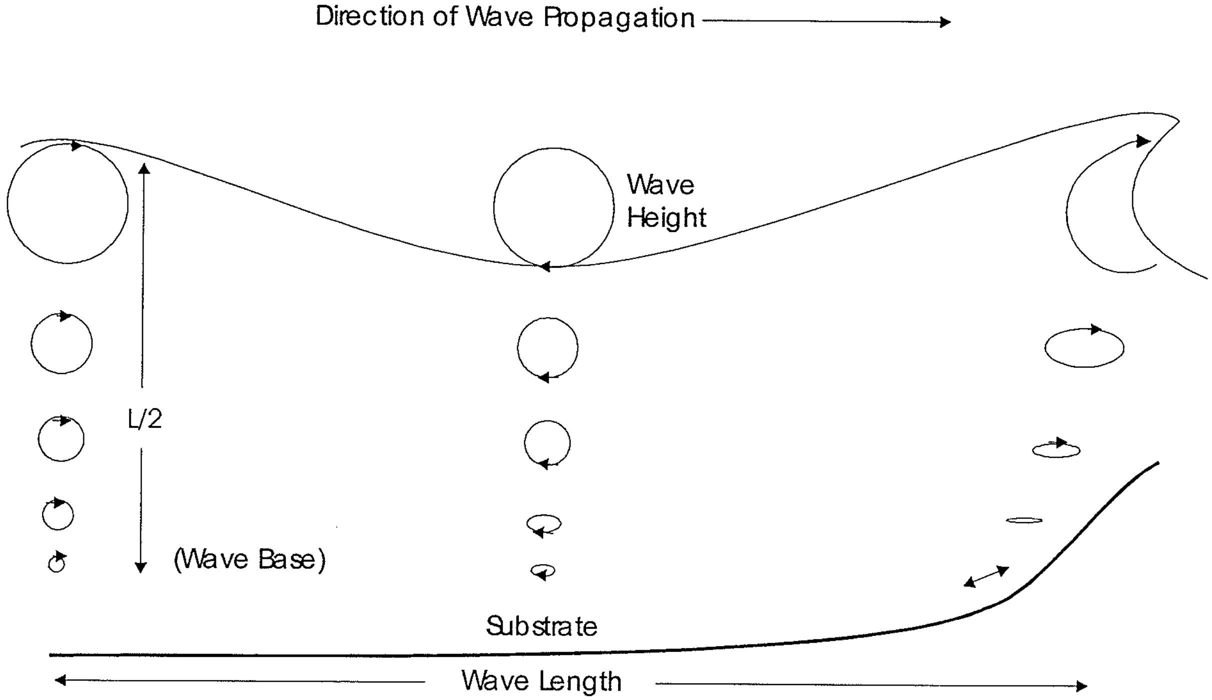

Figure 2.7. The oscillatory orbital motion of a deep water wave attenuating with depth, and change in waveform due to drag induced from wave/substrate interaction.

When a wave contacts the bottom, the orbital movements of the water molecules near the substrate experience friction, which deforms the wave shape and causes it to crest, or collapse. Deep water waves occur in areas of lakes where the water depth is greater than one-quarter the wavelength, and exhibit a sinusoidal form on the surface because the orbital motion of the water molecules is unaffected by the lake bottom.

As a shallow water wave moves towards a shoreline the water depth decreases and the drag induced from the bottom causes the orbital motion of the water molecules to elongate into an elliptical form because the base of the wave moves slower than the crest. This causes the wave height to increase until the wave front becomes too steep for continued stability, and cresting occurs. The physical form of waves determines how their kinetic energy is released. The variables that influence the form of waves are complex but well understood.

2.1.1.3.1.3 Surface Wave Form

The height and period of surface waves depend mainly on the wind velocity and duration (Selby 1990), and the shape and size of the basin (Hutchinson 1957). The strength of the wind and the length of time the wind blows is the major determinant of the amount of energy transferred from the wind to the lake. The morphology of the basin controls the orientation of the lake to the predominant wind direction (Hakanson 1977).

The theory of wave properties is a large and complex body of literature that comprises the detailed study of fluid dynamics, and is beyond the scope here. The principles described here have permeated other scientific disciplines and have demonstrated applicability to this research.

Theoretical and empirical wave energy models often employ fetch distance as a scaling variable. Fetch distance is defined as the linear distance over which a wind travels over water uninterrupted by land. A relatively simple and frequently used method for estimating properties of surface waves is Airy deep water wave theory (Airy 1845).

2.1.1.3.1.4 Deep Water Wave theory

Airy deep water wave theory provides estimates of wave properties including wave length, height, and depth to the sub surface wave base, for sites with an error of < 5% where depth (h) > 0.25 deep water wavelength (L) (Komar 1976). These equations indicate the depth to the sub surface wave base for waves under maximum conditions in water deeper than 0.25 the wave length. Therefore, where this depth boundary occurs on a littoral area, the zone shallower than this depth may be erosive, and depths greater than this could be expected to be deposition. However, a maximum wave event is rare. On the Laurentian Great lakes this occurs only every 10 – 15 years (Saluesleja 1976), suggesting that deposition in shallow water may occur above this depth limit more frequently than it is removed. Rowan et al. (1992) recognized this and developed a model from observed sediment data from temperate lakes and found that 77% of maximum conditions best described depositional boundaries. They reported that wind/wave events of this magnitude occur a few times each year.

2.1.1.3.1.5 Wave Refraction: shoreline form and the distribution of wave energy

A wave propagating towards the coast with geological headlands first experiences sub-surface friction at depth in front of the headland. The shape of the wave front becomes refracted because most of the same wave crest is in front of the beach in deep water and travels at the speed of a deep water wave. The shape of the wave front changes from parallel to the shore in deep water, to a curved shape that is concentrated on the headland (Figure 2.8), changing how kinetic energy is expended.

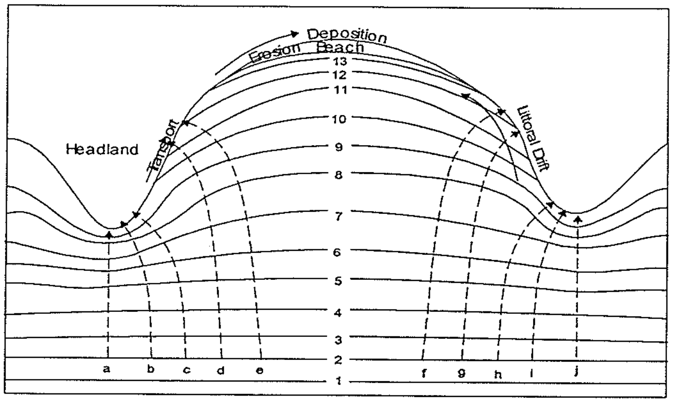

Figure 2.8. Wave refraction (dashed lines, a-j) of wave crests (numbered 1-13) on an embayed shoreline, and the resultant erosion-transport-deposition of materials from littoral drift. Modified from: Strahler and Strahler, 1978.

The distribution of energy changes from a concentrated high energy-erosive wave at the headland, to a weaker and dispersed deposition wave in the bay. This resuspends and moves shoreline materials mostly in two directions: offshore, and along the shore.

The decrease of hydraulic energy in offshore and longshore directions forces gradients of response in the form of substrate material size distributions. Headlands have the highest nearshore slope and largest substrate materials of the embayment. As the bed materials move, an equilibrium or steady state (Selby 1990) is established between material size, the incident wave energy, and the resultant slope. As a result, the form of shorelines and littoral areas in areas that are shaped by wave energy have cusped shoreline shapes, and exhibit particle resuspension, transport, and deposition in deeper water below the effect of waves. The depth of mixing is dependent on the size of waves but the spatial patterns that result are common to embayments and so are scale independent. The diversity of shorelines we observe results from the erratic nature of regional geology, and the redistribution/sorting of materials by water movements. This process creates zones that have frequent water movement, to others that are standing water.

2.1.1.3.1.6 Lake Currents

Currents in Lake Malawi are poorly known. Surface currents are generated by circulation of the atmosphere and earth's rotation which interact to produce wind driven circulation (Davis 1987). Owen and Crossley (1989) report that in the southern basin of Lake Malawi, bottom currents are active through axial distribution of fine sediment units. Ribbink et al. (1983) state that divers at times have needed ropes to move up current, indicating mass movement.

Without information about data on water mass movement it is difficult to assess the relative importance of surface waves, or lake circulation, at any given site. However, in shallow temperate lakes, Hawley and Lesht (1992) state that wave shear stress was 3-10 times that of current stresses. Often during the year shear stress on the bottom due to waves was zero (insufficient wind forcing) but that current shear stress was never zero. It appears that shallow water sites are most likely to be reworked by surface wave energy.

Owen and Crossley (1989) also note that evaporative cooling of surface water in Lake Malawi occurs in late May when the cooler windy period begins. Profile-bound currents result from subsidence of dense water from wind-induced surface cooling, and produce erosional moats around rocky pinnacles that rise from the lake floor. In Japan, a thermocline seich was observed by Chunmeng and Kumagai (1995). They measured currents sufficient to mobilize sediments at 50 m depth in Lake Biwa when a thermocline wave developed following passage of a typhoon.

2.1.1.4 A Variable of Response: the distribution of sediments

Sediment in lakes arises from allocthonous (outside-lake) or autochthonous (within-lake) sources. The sedimentation of fine particulate material (silt-clay) from the water column is caused primarily by cohesion between particles obtaining a density sufficient for deposition (Hakanson 1977). The dynamic behavior of silt and clay in shallow areas of lakes is important since these particles may settle to the bottom, and repeatedly be resuspended into the water column (Luettich et al. 1990).

The distribution of sediments in lakes has long been recognized to be distributed unevenly, with greater accumulation in the deeper areas (Wilson 1938, Wilson and Opdyke 1941), on the lake bed. Likens and Davis (1975) termed this process sediment focusing, which conveys the effect of numerous processes that tend to transport sediments to deeper areas of lakes. Particle size and water content of a benthic sample are inversely related. The measurement or classification of sediments tends to use water content (Hakanson 1977, 1981), mean sample grain size (e.g. phi, Rowan et al. 1992, Rasmussen 1997).

Deep water sedimentation often occurs below the effect of surface waves (Rowan et al. 1992, Cooley 1999) and reveals that the slope of the lakebed interacts with the tractive force of gravity to transport materials. Hakanson and Janssen (1983) show that depositional slopes are usually less than 3%, slopes greater than 4 - 5% exhibit transport of fine sediments by gravity but slopes greater than 10% usually are free of fine sediments.

2.1.1.5 *Physical Habitat Summary*

At the smallest spatial scale and longest temporal scale tectonic process sets the general framework (i.e. shape and size) of the Lake Malawi basin. This "basin" scale largely determines the distribution and availability of coastal and littoral materials and slope.

The lake shape and size factors for Lake Malawi are set within a regional climate that varies with latitude, elevation, and season. Climatic forcing functions control the temperature, evaporation, lake level, and transfer of wind energy (direction, periodicity, and magnitude) to the lake surface. The variations of wind variables determine the potential of an area to achieve maximum surface wave energy. This sets the maximum size of materials that can be redistributed by surface waves, and the maximum water depth of mixing and lakebed resuspension. Persistence of any one of the wind forcing variables may cause a net movement of surface water within the basin and form internal waves which also swash and backwash on the coast at depths determined by the thermal/chemical structure of the water.

Redistribution of available materials by surface waves operates within the geological framework set up at the basin scale, and consequently, material redistribution is often segmented along the coast. Material sorting by size occurs horizontally and vertically due to wave refraction. The extent of this sorting is scale dependent and is determined mostly by the basin scale geology and fetch distance.

At the largest spatial scale, the substratum distribution results from the complex combination of all variables at all spatial and temporal scales. The spatial pattern, or response of the substratum to this physical forcing is known as erosion, transport, and deposition, and is scale independent.

2.1.2 Methods for Acquiring Coastal and Littoral Data

Coastal and littoral habitat data are challenging to collect due to the extensive, yet narrow, geometry of the coast. Also, the littoral substratum cannot be viewed directly and spans a wide range in depth. This section describes methods for acquiring coastal and littoral habitat data. In particular, I review select visible/infrared sensors, synthetic aperture radar[3] (SAR), and acoustic methods of remote sensing and their underlying principals in order to evaluate them as way to collect this data.

2.1.2.1 Remote Sensing of the Coastal Zone

Active[4] and Passive[5] forms of remote sensing have demonstrated utility in a wide range of natural resource applications. Choice for a satellite platform to collect data often is based on the size of the target materials, the electromagnetic properties of the material, and the timeliness of the platform to provide reliable image data. Passive remote sensing within the optical portion of the electromagnetic spectrum is constrained to daylight and requires cloud free conditions. As described below, there may be merit to study comparatively the coastal zone of Lake Malawi in the optical and microwave portions of

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[3] Radar refers to radio detection and ranging

[4] Active remote sensing refers to an instrument that sends a signal to a target and then receives the reflected signal.

[5] Passive remote sensing refers to an instrument that measures a signal emitted from a target.

the spectrum because timely image acquisition is essential and differences in the optical portion of the spectrum are clearly evident.

2.1.2.2 Satellite Remote Sensing of the Coastal Zone

Synthetic aperture radar (SAR) imaging offered by the RADARSAT-1 satellite offers potential for coastal application in the tropics as it operates at a microwave frequency that is independent of cloud cover, daylight, and offers a high spatial resolution. However, the use of SAR in coastal studies has been limited, exploratory, and encumbered with technical considerations (e.g. Barbosa et al. 1999, Werle and Tittley 1997, Gray, et al. 1997, Singhroy 1996, Monakhov and Shubina 1994, Dugan and Mied 1993) suggesting the role of SAR in coastal biodiversity research remains unexplored.

System parameters including incident angle, look direction, and image calibration, can influence the amount of radiation reflected to the SAR (Raney 1998, Ahern and Raney 1993, Gray et al. 1997). Although RADARSAT is designed to exploit optimal illumination geometry between the satellite and target by looking east or west with one of a range of incident angles, at low latitudes its polar orbit results in a limited selection of incident angles for any single image area. This implies that an image mosaic for large areas like Lake Malawi will be derived from images obtained using different look and incident angles. Classification of such images must assume that the effect of system parameters is small.

Coastal zone assessment using optical satellites has a relatively long history. A detailed account is beyond the scope of this section. Most effort has been the study of coastal vegetation (Donoghue et al. 1995, Hardisky et al. 1986, Budd and Milton 1982, Best et al. 1981, Bartlett and Klemas 1981, Klemas et al. 1975). More recently, studies have shown that optical and SAR data together can improve classification of a variety of earth materials (e.g. Yesou et al. 1993, Rigol and Chica-Olmo 1998), and of coastal wetlands (Wang et al. 1997). This suggests merit exists in this approach for lake Malawi. However, to my knowledge, no studies have attempted to discriminate between different coastal attributes using statistical analysis of SAR and optical satellite data.

2.1.3 SAR Scattering and Optical Reflectance of the Coastal Zone

The radar backscatter coefficient (σ°), also called sigma naught, is the most frequently used measure of SAR reflectivity. It is derived from one or more individual reflections and is measured in decibels (dB). Pixels in a SAR image represent point measurements of the σ°, which is related mainly to the size interrelationships between the radar wavelength and the scattering elements in the footprint of the radar resolution. An object that is larger than the SAR wavelength (i.e. 5 cm) is more apparent to the SAR than are those that are not.

Radar backscatter is convolved with a well understood coherent fading signal (Ulaby et al 1986). Fading, also known as speckle (Goodman 1976), in SAR image data is random multiplicative noise that results from the constructive and destructive interference of electromagnetic radiation. Speckle is inherent to SAR imaging and increases the variance of image data. It is recognized visually in imagery as an increased frequency of dark and light pixels in what should be a relatively homogenous grey level field (Barber and LeDrew 1991).

The microwaves backscattered from the coast results from a combination of surface and volume scattering, which is determined mostly by the surface roughness, and the dielectric constant (i.e. electrical properties) of the material. Rocky coasts comprised of boulders are discrete scatterers larger than the radar wavelength, and usually smaller than the radar resolution. A SAR will respond both to the size of scattering elements greater than the wavelength, and to the electrical properties of rock. SAR reflections from rock will be from near the surface (Daily et al. 1979) providing potential for strong backscatter. Rocky coasts appear rough to the SAR.

The grains of sand within a beach are all smaller than the wavelength facilitating penetration of the microwaves in to the volume of the beach. The amount of microwaves reflected back to the SAR may be lower than for rock due to losses from forward scattering within the volume of the beach, and so appears smooth to the SAR. A beach wetted by rain will have a higher dielectric constant, and therefore have an increased component of near surface scattering, thereby increasing the amount of backscattered radiation. Vegetation has a large void volume but relatively high water content, and so will reflect microwaves readily from within the volume of the vegetation. An increase in moisture content may increase the backscatter for all three types of coast.

In general, a surface scattering medium can provide strong radar returns but tends to be spatially more variable than a volume scattering medium due to directional scattering that does not always return back to the SAR. Volume scattering materials tend to have lower SAR returns with less variation among pixels due to diffuse scattering of which some of the reflected field of microwaves reflects back to the SAR. A detailed review of SAR theory and technical considerations is provided by Raney (1998).

As a passive sensor, SPOT relies on the sun for illumination and incoherently measures the reflectivity of objects on the earth's surface using high-resolution visible and infrared sensors. The SPOT 4 satellite provides four multispectral bands: band 1 green (0.50 - 0.59μm), band 2 red (0.61 - 0.68μm), band 3 near infrared (NIR 0.79 - 0.89μm), and band 4 short wave infrared (1.58 -1.75μm). The SPOT sensor and applications data are well described (Jensen 2000).

2.1.4 Acoustic Remote Sensing

A vertical beam sonar system is an active form of remote sensing that is operated from a boat and uses attributes of transmitted and reflected sound waves to define the composition of, and measure the distance to, the floor of a body of water. An acoustic pulse impacting the lake bottom is reflected and scattered at the lake floor/water interface by the material in the immediate sub-surface as a complex function of interrelationships including the size of the objects, porosity (i.e. water volume), and the frequency (i.e. the acoustic impedance) of the emitted energy. As stated above for radar, objects larger than the wavelength are more reflective, and provide more surface scattering. Unconsolidated sediment is a porous and loose structure whose interstices are filled with water. This material will contain a larger transmission component than will sand or rock substratum that will reflect strongly. The strength of the reflected acoustic pulse from the sediment volume will be diminished because part of the energy passes through the sediment volume and is absorbed.

The amplitude and shape of acoustic echoes reflected from the lake bed is determined mostly by the bottom roughness and by the contrast in acoustic impedance between the water and bottom. The amplitude is determined by the energy ratio of the first and second echo reflected from the bottom. When an acoustic wave travels through the water and encounters the sediment boundary of the lake bed, reflected and transmitted waves are generated at the fluid-sediment boundary (Figure 2.9).

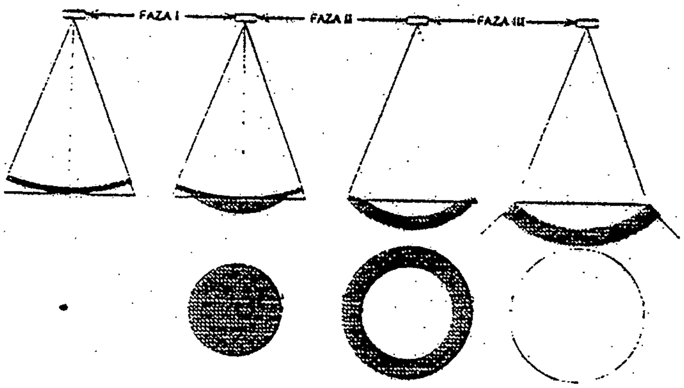

Figure 2.9. Sounding phases of an acoustic pulse. Phase 1: the interval between the front and back reaches the bottom. Phase 2: lasts until the pulse leaves the beam pattern. Phase 3: lasts until the sounding phase has fully penetrated the bottom (Stepnowski 1996)

The signal received in phase 1 comes mainly from specular reflection from the bottom surface, and the signals amplitude is determined by the ratio of acoustic impedance of water and the bottom material. In phase 2 and 3, the sonar transducer receives signals scattered from oblique incident angles on the bottom surface.

The character of the returned echo from the lake floor can be used to discriminate the composition because the shape of the response echo varies both in pulse length and amplitude. A lake floor of low acoustic impedance produces an elongated echo return due to the delay in return time as the acoustic wave reflects from deeper within the volume of the lake floor. Alternatively, when acoustic impedance is high (i.e. a strong reflection coefficient) the magnitude will be larger and the time delay will be shorter. These echo attributes are indicators of bottom "hardness" and "roughness".

For a simple harmonic plane wave normally incident on a plane boundary, the Rayleigh reflection coefficient is often employed to classify surficial sediments in freshwater and marine environments (Leblanc et al. 1992), and the bottom loss (BL) of the plane wave at normal incidence is accounted for by:

$$BL = -20\ \mathrm{Log10}(R)$$

R = the Rayleigh reflection coefficient.

The combination of proprietary signal processing hardware, frequency, cone angle, and varied bottom types and the youth of this technology makes a clear understanding of the effect of these parameters on the echo returns difficult. It appears that the first, more powerful, echo is a better discriminator than is the second (e.g. Stepnowski 1996), and that a narrower cone angle is beneficial in shallow water (Hedgepeth et al., unpublished). Also variability in the bottom composition should occur at scales that exceed the size of the acoustic footprint. Pockets of gas also can confuse classification (Rukavina and Caddel 1997).

Stepnowski et al. (1996) used 38 kHz and 120 kHz to compare the roughness signatures to hardness for rock, sand, soft sand, soft mud. For comparison, they also estimated these parameters for the second echo. Complete separation of the classes was not possible at either of the two frequencies or echoes used. The use of the first bottom echo was superior to that of the less powerful second echo. Visual separation of bottom classes was good. Hedgepeth et al., (unpublished) compared rock, sand, and mud using three frequencies (200 – 400 kHz) at two cone angles (6.2 – 8.9 degrees) in depths up to 15 m using the first echo. Their data show that mud could be separated visually from sand and rock, but sand and rock showed overlap across all trials.

Acoustic mapping of littoral areas of Lake Malawi appears to be the only technique that can identify discontinuities in the substratum over a large range in depth. The potential to reliably discern the rock/sand boundary presently is unclear, but a system that uses the first echo to characterize the bottom within the 38 kHz – 200 kHz range could discriminate the sand/mud boundary. This would provide first insight as to whether the mud boundary in large lakes forms an abrupt transition as it does in small lakes, and mapping of this boundary over large areas would also confirm the consistency of its position relative to slope and depth.

2.1.5 Allopatric and Sympatric Mechanisms of Cichlid Diversity

This section provides an overview of two main mechanisms reported to have contributed to the cichlid diversity in East Africa. The regional emphasis reflects a comparative synthesis of understanding undertaken by the scientific community.

The general modes of speciation for the haplochromine cichlids can be divided into extrinsic and intrinsic factors, which imply either environmental or biological controls for differentiation[6]. Of the 13 physical and biological models of speciation identified by Kornfield and Smith (2000) from the literature, allopatric[7], and sympatric[8] (i.e. sexual selection) modes of speciation appear to be most in favor. Allopatric models contend that geographic variation in characteristics such as morphology or color is

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[6] Differentiation: reductions in gene flow create opportunities for divergent evolutionary trajectories.

[7] Allopatric: species or populations that do not interbreed because they are geographically isolated from one another

[8] Sympatric: species that occupy the same habitat but do not interbreed

generated by colonization of habitats by founders and isolation is subsequently maintained by limited dispersal (i.e. habitat barriers), upon which genetic drift[9] and natural selection[10] operate. The two main forms of allopatry are: 1) macroallopatry in which isolation is achieved via discrete basins, and 2) microallopatry, which is a local process of isolation, effected by distance (Meyer et al. 1994, Rossiter 1995). Sympatric models are also appealing because the limited dispersal abilities of the cichlids studied, and the large size of the lakes implies allopatry alone may not account for the rapid expansion of the species flocks in each of the African Great Lakes (McCune and Lovejoy 1998). Each of these two models of divergence is reviewed in brief below.

2.1.5.1 Allopatric Speciation

The recognition of lake level variation in the African Great Lakes as a macroallopatric agent of speciation is not new (Trewavas 1935, Fryer 1959). The timing of lake level fluctuations reported for Lakes Malawi, Tanganyika, and Victoria is not synchronized within the East Rift (Kornfield and Smith 2000). In Lake Tanganyika, water level declines of about 550 m exposed three isolated sub-basins (Sturmbauer and Meyer 1992) that lead to divergent lineages of cichlids (Sturmbauer 1998), but rises in water level have reconnected the basins as a single lake for more than 21 ky. In the much shallower and single basin of Lake Victoria, initial hypotheses of peripheral "satellite"

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[9] Genetic drift: the changes that occur in the gene frequency of small, isolated populations, resulting in the loss or preservation of certain genes over generations.

[10] Natural selection: an adaptive process, according to Darwin, by which organisms best suited to survive in a particular environment pass those desirable traits to succeeding generations.

lakes (Greenwood 1965) were thought to have contributed refugia during low stands. Geological evidence suggests that the lake dried out completely about 14, 700 years ago (Johnson et al. 1996) suggesting rapid speciation. However, recent genetic and phylogenetic studies reveal the origin of the cichlid flock of Lake Victoria appears to have been derived from an older (100 000 year old) lineage from Lake Kivu (Verheyen et al. 2003) that apparently reseeded the lake after desiccation. In the case of the two basin but deep (>700 m) rift of Lake Malawi (Cooley 1998, Cooley et al. 2000), little has been added to the early hypothesis of divergence based on philopatry[11] and distance by Fryer (1959), except for the shallow southern basin where debate has arisen.

The shallow southern region of Lake Malawi contains 62 species of endemic mbuna (compiled from Ribbink et al. 1983) that are found mainly on islands or rocky pinnacles where rocky substrata are most abundant. Desiccation of the southern basin 120 m below the present level during the period 1500 – 1850 was claimed by Owen et al. (1990) via several lines of indirect evidence including sediment analysis, and hydrological modeling. Endemics of this region either speciated in just a few hundred years, or these species became extinct in their former ranges after colonizing the newly flooded habitats. This has magnified the already contentious issue of the rate of speciation in African cichlid fishes. More recently, studies suggest low lake stands in lake Malawi could be older. Delvaux (1995) reports the age of the last major low lake stand was 250 to 500 m below present between 42,000 and 25 - 11,000 years ago. Lake level drops on the order of 100 – 150 m occurred 5 – 10 000 years ago Ricketts (1998).

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[11] Philopatry: a species with limited dispersal abilities or range requirements; occupies a small niche.

Uncertainty in the temporal resolution of these estimates suggests other ways to improve our ability to perceive geographic pattern within the lakes should be explored. If patterns of species distributions are interpreted to better understand allopatry in the Rift Valley, a real need exists for lake wide habitat distributions. To understand habitat availability under scenarios of fluctuating water levels, a better understanding of the effect of landform on the expression of habitat characteristics is essential.

Microallopatric divergence has been shown in Lake Tanganyika, as a result of secondary contact between divergent populations (Fryer and Iles, 1972). For the mbuna of Lake Malawi, we have little evidence that enables us to define what type or length of a habitat discontinuity is required to form a barrier to dispersal. Hert (1992) found tagged territorial male mbuna of several species could find their home sites from up to 2.5 km away when translocated along a continuous rocky coast. When translocations along rocky coasts were compared to those of open water at distances of about 500 m, Hert showed successful homing occurred for both trials, but fewer of the individuals returned home from open water. Translocation to a sandy beach 1 km away and separated by deep water resulted in no returns. Ribbink (1978, cited in Hert 1992) showed that mbuna adapt poorly to rapid pressure changes and so are unlikely to follow the bottom across deep water areas. Recently, on the Usisya Border fault at Ruarwe, Rico and Turner (2002) showed significant genetic differentiation in allele frequency for demes of a single mbuna species found on either side of a 35 m long sandy coast containing a tributary. Interestingly, they suggest the 5 degree drop in temperature provided by the rift scarp inflow during September may have been a more significant barrier to movement than the sandy coast because similar studies of the same species by Van Oppen et al. (1998) at Nkhata Bay showed stronger genetic similarities over much longer habitat discontinuities. However, the year round persistence of this thermal gradient was not demonstrated, and during June this gradient did not discourage several species of Lethrinops from creating bowers (excavated sand nests) in front of this tributary (A. Konings, pers. Com). Along the Livingstone border fault, Spreinat (1995) noted that many of the mbuna species do not have a segmented distribution and are found along its entire length. These examples appear to suggest that biologists have taken a species approach in a set of arbitrary locations. To better understand microallopatry, it may be preferable to develop information on local habitat distributions paired with local species distributions.

2.1.5.2 Sympatric Speciation

Current models of sympatric speciation in the African Great Lakes differ from traditional ones where ecological differences promote co-occurring, reproductively independent species. In these lakes, closely related haplochromine species appear to occupy similar ecological niches so sympatric differentiation is presumed to occur not by mechanisms of rapid ecological divergence, or differences in habitat preference (Kornfield and Smith 2000). The ability of female cichlids to discriminate colored males of their own or closely related species (Holzberg 1978, Knight and Turner 1999, Knight et al. 1998, Seehausen, and van Alphen. 1998, Seehausen and van Alphen 1999) is important to maintain diversity, especially where closely related species are sympatric and occupy a similar ecological niche.

Under these conditions, Seehausen et al. (1997) provided a persuasive hypothesis that could explain the high frequency of speciation events for the rock dwelling Mbipi in Lake Victoria. They show that choice of mate coloration of males by females maintains reproductive isolation of sympatric species and color morphs[12]. The hypothesis of sexual selection is favored because it appears to explain the continued maintenance of overlapping distributions after allopatric speciation and it also allows for full in situ sympatric speciation (Galis and Metz 1998). VanOppen et al. (1998) tested the assumption that sympatrically occuring males of different colour represent biological species using behavioral observations and microsatellite DNA analyses for 6 species. They found that most species showed clear assortative courtship and little or no gene flow between populations. Relatively clear water is essential to maintain mate recognition. Unfortunately, decreases in water quality in Lake Victoria have reduced transparency and this appears to break down this reproductive barrier resulting in hybridization (Seehausen et al 1997). Note, however, that in an allopatric context, Smith and Kornfield (2000) consider hybridization to increase species diversity!

2.1.6 Systematics and Taxonomy

A detailed account of the taxonomy and systematics of the African Great Lakes, or Lake Malawi in particular, is complex and beyond the present scope. Rather than attempt a superficial discussion of a complex and rapidly evolving topic, I provide below a short summary of recently published works, mainly by Jos Snoeks the principal

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[12] Colour morphs: a species that has more than one coloration.

taxonomist of the Lake Malawi Biodiversity Conservation Project. Dr. Snoeks is among the world experts in African cichlids. His experience and knowledge of the intricate complexities in naming cichlids sets a rational tone to applying discreet structures to gradients of evolution. He has already published two papers that describe why this section cannot easily provide as detailed an account as one might wish, or if it was attempted, why it would become obsolete so quickly. I refer the reader to Snoeks (2000, 2001) where the challenges faced by cichlid taxonomists are elaborated and from which this section was based.

The cichlid fauna in East Africa is unique because of the large number of species present and exceptionally high endemism. The family Cichlidae has been reported as the third largest family of fishes in the world (Nelson 1994) but a new conservative estimate (Kullander 1998, Snoeks, 2000) of 2,400 species suggests the cichlids comprise the largest family of fishes, and even of vertebrates (Snoeks, 2001). Approximately 550 cichlids inhabit Central and South America (Kullander 1998), but it is in East Africa where cichlid speciation is unparalleled. The lakes of East Africa contain more than 10% of the extant freshwater fishes of the world, and each of the three great lakes (Victoria, Tanganyika, and Malawi) has more fish species than any other lake on Earth. As noted earlier, the fish species richness of Lake Malawi is highest and is estimated to have 847 species. All of the species in Lake Malawi are haplochromine cichlids, except for 47 non-cichlids.

The term haplochromine originally meant species classified in the genus Haplochromis. This was later subdivided into many genera as more species were discovered, better described, and reclassified across East Africa. Today the whole group is loosely referred to as Haplochromine to recognize a common perceived phylogenetic lineage. Haplochromines exhibit share similar morphological characters, are maternal mouth brooders, and are polygamous. Generally, it is the males who display the egg spots and the colors that attract and entice females.

Identification of cichlid species in Lake Malawi remains difficult because the fishes are so similar in appearance. At present, about two-fifths of the Malawian haplochromine fauna have been described and many are differentiated by color. Snoeks (2001) relays that the easy species are named first, and the difficult ones gain in number over time. It is not that easy to identify species are abundant and/or widespread, nor is it that difficult to identify species are rare. Understanding of the Malawi fauna is far from complete and many geographic areas remain unsurveyed, especially in deep water. Samples from unstudied areas yield many new species, and well studied sites still yield new species.

As new species are discovered the taxonomic picture changes not only at the species level, but also at the genus level. In Lake Malawi, the classification of the haplochromine genera is based on the melanin pattern and on morphological features (Eccles and Trewavas 1989) and this sometimes leads to conflicting views of taxa. Additionally, phylogenetic studies now include new methods from molecular biology. While mitochondrial DNA sequencing has yet to demonstrate unambiguous taxonomies in recently evolved flocks like the one from Lake Malawi, it is more apparent than ever that multiple methods rarely provide the same taxonomic affinity.

The question "How many species are there in the lake?" skirts the real question about the phylogenetic trajectories of the species, and this must be addressed before any meaningful (unchanging) species number for the scientifically described taxa can be provided. Because the phylogeny of the Malawi species flock is still poorly understood, the underlying evolution is largely unappreciated. In this regard, Snoeks feels that the growing number of species sampled recently reveals a trend “from chaos to greater complexity”.

2.2 Conclusions

In Chapter 2, I introduced elements of the physical geography of the Lake Malawi drainage basin, methods to acquire habitat information, and described two main mechanisms that contribute to haplochromine diversity.

The process of erosion, transport, and deposition sorts earth materials by size and results from a suite of environmental variables that operate at all spatial and temporal scales. A difference in the observed composition or pattern of the earth materials reflects changes in the relative number, magnitude, and frequency of the forcing variables. The objective of the physical geography and habitat section was to describe and illustrate the linkages between the climatic, tectonic, and geomorphologic framework of the basin in setting up the lake level and availability the of materials at the basin scale, and that the within lake variables that form physical habitat are limited by the system scale and regional variables. Several subsections illustrated these variables in terms of forcing and response.

A section illustrated applicable technologies for acquiring coastal and littoral data including remote sensing using satellite and boat-based platforms. It was concluded that remote sensing could provide a valuable means for collecting data from large tropical lakes while SAR and acoustic remote sensing potentially could provide data for large areas or a large range in depth but remains unexplored. In particular the acoustic separation of sand and mud in deep water appears feasible.

Two mechanisms for haplochromine speciation in Lake Malawi, i.e. allopatric and sympatric speciation, were reviewed for the African Great Lakes. The objective of this section was to illustrate these mechanisms and tie in the effect of lake level variation as a possible mechanism for allopatric divergence; this links a biological process to a regional climate process. It was noted that the timing of the last low lake stand was uncertain, and merited further study. It was concluded that other complementary means of interpretation, such as direct and coupled observation of habitat and species distributions, could help to assess the roles of speciation and any effect of water level variation on the haplochromines. This review was based mostly on the fishes of the rock shores from each of the three great lakes because little information exists for fishes inhabiting sand, except for the studies by Greenwood.

Chapter 3 Remote Sensing of the Coastal Zone of Lake Malawi using Synthetic Aperture Radar and Optical Data

3.1 Introduction

In this chapter I present an analysis of the effects of coherent fading, look direction, and incident angle of Synthetic Aperture Radar on rock, sand, and vegetated coasts to assess the potential for a remote approach to coastal zone discrimination and classification. The analysis includes the more familiar optical data for comparison. The use of SAR information in general is in its infancy but coastal studies with both sensors have been biased towards wetlands. No studies have attempted to discriminate between different coastal attributes using statistical analysis of SAR and optical satellite data. The particular merit of Synthetic aperture radar (SAR) imaging offered by the RADARSAT-1 satellite offers potential for coastal application in the tropics as it operates at microwave frequency that is independent of daylight, the ubiquitous cloud cover, and offers a high spatial resolution.

System parameters including incident angle, look direction, and image calibration, can influence the amount of radiation reflected to the SAR (Raney 1998, Ahern and Raney 1993, Gray et al. 1997). Although RADARSAT is designed to exploit optimal illumination geometry between the satellite and target by looking east or west with one of a range of incident angles, at low latitudes its polar orbit results in a limited selection of incident angles for any single image area. This implies that an image mosaic for large areas like Lake Malawi will be derived from images obtained using different look and incident angles. Classification of such images must assume the effect of system parameters is small.

In this chapter, I use a case study to illustrate the potential for coastal zone mapping. The research questions I address within this framework are designed to assess the importance of system parameters, or lack thereof, in determining what imaging modes can be used while also revealing the relative capacity of SAR and optical data to discriminate and classify the coastal zone. The principal objective of this chapter, therefore, is to provide an informed decision making capacity to determine if remote sensing can be used effectively to classify the entire coast of Lake Malawi. The results of this work are found in the peer-reviewed literature Cooley and Barber (2003a). The specific objectives of this chapter are to:

1) *Assess the effects of incident angle and look direction on SAR backscatter for each class. To do this I test the null hypothesis that the SAR backscatter is equal within each of the rock, sand, and vegetated classes among the SAR system parameters (look direction and incident angle).*

2) *Assess if SAR backscatter can be used to effectively discriminate and classify rock, sand, and vegetated coasts. I use radar backscatter and geometric variables that can be obtained from the images and on-site measurements, and compare classification by these means to the classification of SPOT.*

3) *Assess the merit of combining SAR + SPOT to evaluate an entirely remote approach to discrimination and classification.*

3.2 Methods

3.2.1 Study Areas

Rock, sand, and vegetated coasts were surveyed in two areas of the southern basin of Lake Malawi (Figure 3.1). Lakeshores in area 1 are dominated by sand beaches with slopes less than 4.6° (7.2 km), dense stands of vegetation, Phragmites mauritianus, 2 – 3 meters in height overlying nearly level sand platforms (9.7 km). Rock coasts are characterized by rounded granodiorite boulders usually ranging in size from 1 – 3 meters, with coastal slopes ranging 7 - 30 ° (area 1: 2 km, area 2: 12 km).

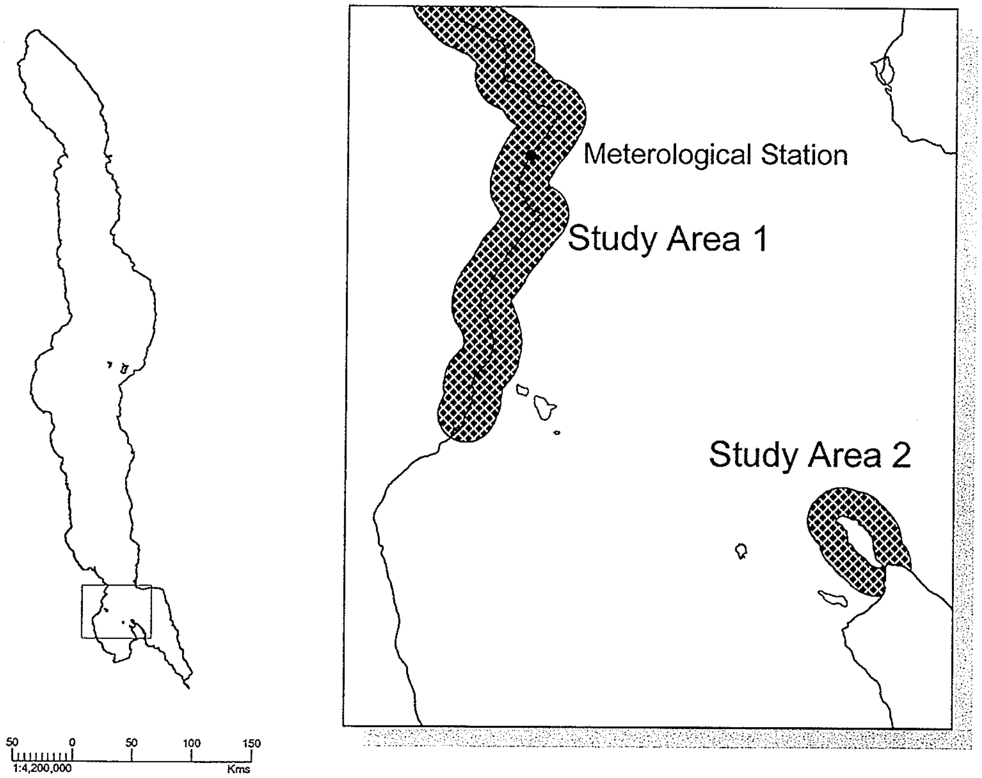

Figure 3.1. The location of study areas 1 and 2 in the southern basin of Lake Malawi. The location of the meteorological station is shown.

The region is sub-tropical with a seasonal climate. During this study the dry season extended from June to late November. The rains (and cloud cover) increase in frequency and intensity by mid-January. Precipitation shows a diurnal pattern with more rain occurring at night (Pegado 2000). Lake levels are controlled mainly by evaporation during the dry period, and vary about 1 meter annually (Patterson and Kachinjika 1995). The best potential for remote sensing of the coastal zone in Lake Malawi occurs during the onset of the rainy season (late December/early January) when the lake level is lowest.

3.2.2 Image Data

Eight RADARSAT fine beam (SGX) images were acquired for the two study areas during a 13 month period from 1996 – 1998 (Table 3.1). Six of the eight images were captured during the month of December. A single multispectral SPOT 4 image was acquired during dry and warm weather in November 1998 with no visible clouds or haze.

Table 3.1. RADARSAT fine beam (SGX) images acquired at high and low incident angles for each look direction in two study areas. The pixel spacing of SGX data is 3.1 meters. Beam modes (F1F – F5F) correspond to nominal incident angles. The pixel spacing of the SPOT data is 20 m.

Study Area	D/M/Yr.	Beam Mode	Incident Angle Class	Orbit	Local Time
1	09/12/97	F2F	Low	Desc	01:06:27
1	16/12/97	F5F	High	Desc	01:06:27
1	18/12/97	F4F	High	Asc	14:15:48
1	25/12/97	F1F	Low	Asc	14:11:40
2	23/12/96	F5	High	Asc	14:15:55
2	30/12/96	F 2	Low	Asc	14:11:47
2	02/01/98	F2N	Low	Desc	01:10:39
2	09/01/98	F4F	High	Desc	01:06:30
1	15/11/98	SPOT	-	-	10:12:00

To test the similarity of σ° estimates among look and incident angles, four fine beam SAR images were acquired for each study area, representing high and low incident angle images for each west and east look direction. Fine beam data are referred to as single look and provide the best spatial resolution available from the RADARSAT system. The azimuth resolution is 8.4 m, with range resolution from 9.1 m to 7.8 m. Fine beam data have a pixel size of 3.1 metres. The pixel size of radar data is not the same as spatial resolution, and is explained in Raney (1998). The 15 fine beam imaging modes capture imagery with an incident angle range from 35-49^0. Each image represents an incident angle range of less than 3.2^0. Image modes are designated F1 to F5 to indicate low to high incident angles, respectively. Each of the five nominal fine beam modes is complemented by two others, offset slightly in the near and far range. For example, an F2N and F2F designate a fine 2 near beam and a fine 2 far beam. SPOT data has a pixel size of 20 m.

3.2.3 Field Surveys and Data Processing

I mapped the perimeter of 31 km of rock, sand, and vegetated coasts, using Global Positioning Systems (GPS) during the period of seasonal low water levels. On sand beaches and smaller stands of vegetation, shoreline polygons were collected by walking one meter inside the perimeter of the feature. Traversing was not possible for the boulder coasts and dense stands of vegetation. In such areas, point features were collected at the shore/water interface using the average of 30 GPS positions every 50 m along the coast. All GPS data were differentially corrected and validated as sub-meter by comparison to trigonometric reference stations in the region (Cooley et al. 1998).

Shoreline ground control points, (GCPs) were determined to co-register the coastal GPS data and satellite images. GCPs were determined in each area by averaging 180 positions collected at one - second intervals at the shore water interface. GCPs were collected on individual boulders that were identifiable in the images. For each shoreline polygon, the slope angle of the coast was measured (+/- 0.25 degree) with a hand held Funuto inclinometer. The width of the boulder coasts was measured using a laser range finder (+/- 1 meter).

Forty-three GCPs were collected in study area 1. Fifty-eight GCPs were collected in study area 2. A minimum of 10 Ill defined and distributed GCPs were used in the linear transformation model for each image. The Root Mean Square Error of the models for the 8 SAR images ranged from 0.83 – 1.69 of a pixel, and for SPOT was 0.64 of a pixel.

I did not georeference our coastal images because this process can change pixel values. Instead, I used only original pixel data by transforming the GPS polygons from

Universal Transverse Mercator (UTM) to the arbitrary coordinate system of each SAR image, using a linear transformation model. Rock and vegetated shorelines were interpreted in the imagery visually between the GPS point positions in the arbitrary coordinate system of each image. Reverse transformation models were used to map the arbitrary shoreline coordinate data into UTM, where a buffer zone of the minimum width observed in the field (boulder 25 m, vegetation; = 60 m) was used to delimit the terrestrial bounds of the shore. To reduce data volume, image noise, and to facilitate statistical tests the length of GPS coastal polygons, which extended as long as 3 kilometers, was reduced to a consistent interval of 150 m.

3.2.3.1 Adaptive Filter Sensitivity Trials

Separating SAR image variance into signal and noise (Porcello et al. 1976, Lee 1983, Lee 1986, and Hirose et al. 1989) is difficult. Adaptive filters are often used to minimize SAR image noise. Adaptive filtering of image data removes or averages pixel values greater than a standard deviation threshold derived from a local window of pixels. To reduce speckle, I use the adapted Lee filter of Eastman (1999), derived from Eliason and McEwen (1990). This technique retains fine detail, edges do not become blurred, and preserves the mean value of homogenous areas within 0.1 dB (Lee 1986).

An adaptive filter sensitivity trial was designed to assist in the selection of a standard deviation threshold for our SAR data. A series of thresholds were used on a randomly chosen image to show change for each class in 1) the number of pixels that exceeded the threshold, 2) the $\sigma°$ frequency distributions, and 3) class means. To do this, a single SAR image was selected randomly and a 3 x 3 adaptive filter (which did not exceed the width of the coast) was passed through the source image six times. Each trial processed the raw image data and increased the threshold by 0.5, providing images with a range in standard deviation from 0.5 to 3.

The number of pixels/class that exceeded the standard deviation threshold for each trial was identified in the output image. The total number of pixels greater than the threshold for each class was determined using image cross-tabulation. For each trial, the mean σ° was estimated for each class. Frequency plots were produced for each class and trial to identify visually the parts of the data distribution that exceeded the thresholds. For statistical discrimination a 3 x 3 adaptive filter was used due to the limited width of the coast. The pixel values greater than the chosen threshold were replaced with averages.

The number of pixels identified as noise increases as the standard deviation threshold decreases. A threshold of 3 or 0.5 retains 95 and 20 percent of image pixels, respectively. The mean σ° for each threshold was: rock (-8.2 to – 7.6), sand (-19.05 to -16.04), and vegetation (–11.71 to -10.08). Pixels that exceed the thresholds occur most frequently in the low dB range. Weak returns suggest a component of forward scattering away from the SAR. A conservative threshold of 2 standard deviations retains 90% of image data and was applied to each of the eight images used in the analysis.

3.2.3.2 *Geometric and Reflectance Variables*

In order to investigate the degree to which the reflection of SAR returns may be influenced by the geometry between the SAR instrument and target (Franklin et al. 1995), the angle of each shoreline segment relative to the look direction was calculated using

Computer Aided Design software. Each shoreline segment was assigned this angle, called declination, where 180° is equal to the look direction.

Average SAR $\sigma°$ and SPOT reflectance values were extracted from each shoreline segment, and loaded into a data table for statistical analysis. The variables included: shoreline segment number, class, look direction (ascending/descending), incident angle (high/low), filtered $\sigma°$, declination, coastal slope, and average reflectance values for SPOT bands 1, 2, 3, and 4.

3.2.4 *Univariate Analysis of SAR Backscatter*

Analysis of Variance (ANOVA) was used to test for effect of incident angle and look direction on $\sigma°$ from the coast after tests for normality and heterogeneity of variance. A Scheffe's test matrix of pair wise comparison probabilities was used to isolate the source of significantly different radar returns ($P< 0.05$) by incident angle and look direction. Similar $\sigma°$ estimates for each class were pooled prior to an ANOVA to determine if rock, sand, and vegetation were statistically separable. The variance among classes was stabilized by taking the absolute value of the square root of $\sigma°$.

3.2.5 *Multivariate Discrimination and Classification*

The SAR and optical satellite data are investigated using Multiple Discriminant Analysis (MDA) (Manly 1994). The MDA technique can be used not only to create a predictive classification model that can be applied in other areas of Lake Malawi, but also to understand the relative importance of the variables included in the classification. A predictive model of membership in rock, sand, and vegetated coastal classes (*k*) was developed based on the linear combinations of the available radiometric, geometric, and environmental variables (p) that best discriminates among the groups. The data table containing radar σ° averages, declination, slope, and reflectance digital numbers from each of the 4 SPOT multispectral bands was used to obtain two linear composites that maximally separate each coastal class. The number of discriminant axes is the smaller of $k - 1$ or p. Like the one way ANOVA, the MDA maximizes the F ratio by forming linear composites that maximize the inter – to intra - class variation over *k*.

I first use MDA to demonstrate the relative importance of the radiometric and geometric variables. I then employ a second series of discriminant analyses in which I assume that declination and slope data are unavailable and use only the radiometric values from SAR and SPOT. Discriminant analysis of the SAR and SPOT are treated independently, then combined to assess potential improvements to discrimination, and classification agreement.

Class discrimination is assessed in all cases using 33% of the data to predict class membership for 67% of the remaining data for which membership is known. These are referred to as the model and test groups, respectively. The model group was populated using every third observation in the database, ensuring representation from all study areas. The agreement between predicted group membership and the validated classes was assessed using cross-validation. The analyses containing optical data are limited to study area 1.

3.3 Results and Discussion

3.3.1 SAR Data

Raw SAR data (unfiltered) for 80 adjacent pixels of each class is shown in Figure 3.2. For each class a large range in $\sigma°$ and overlap with the other two classes is apparent. Rock returns are highest, and may range to the upper and lower operational limits of the SAR. On average, vegetation returns are lower than rock. The lower vegetation returns are similar to the lowest returns from rock, but are more frequent. The highest $\sigma°$ for vegetation occurs less frequently than $\sigma°$ for rock. Sand coasts provide returns that are lowest, and relatively few of the raw pixel values overlap with the other classes.

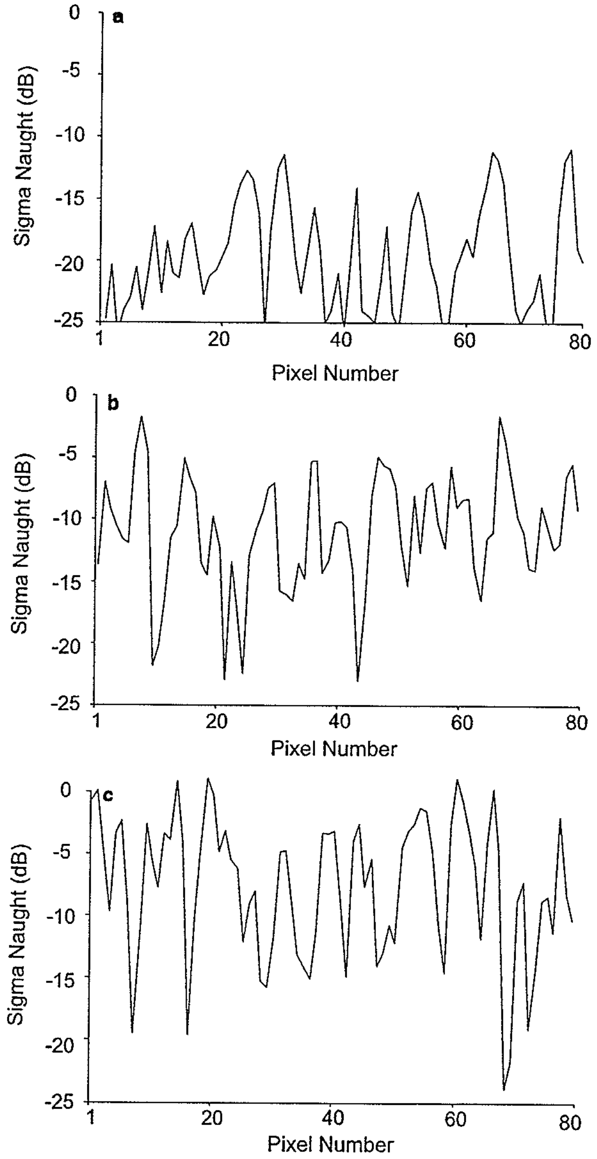

Figure 3.2. SAR backscatter pixel values (dB) for a profile of 80 adjacent pixels in (a) sand, (b) vegetation, (c) rock representative of unfiltered returns derived from fine beam (SGX) RADARSAT data.

3.3.2 *Univariate analysis of SAR backscatter*

Radar shadow was observed along rocky coasts adjacent to topographic relief as dark areas lacking a discernable coast, and was removed from the analysis. This included ascending data from rock coasts in Area 1, and for the west (descending pass) and east (ascending pass) coasts of the island in Area 2. For each of the rocky coasts studied, it can be shown that data suspected as being radar shadow was tested and determined significantly different from the coasts that faced towards the satellite.

Rock, sand, and vegetated pixel averages (n= 606) from the shoreline segments for each SAR image are Gaussian (Shapiro-Wilk; rock p range = 0.43 – 0.93, df range 17-31, sand p range = 0.71 - 0.91, df = 49, vegetation Kolmogorov-Smirnov p range = 0.17 – 0.2, df = 66). Each class has equal variance (Levene; sand p = 0.07, vegetation p = 0.54, rock area 1 p=0.93, rock area 2 p=0.054) except for F2N rock.

Results of the ANOVA are listed in Table 3.2 and shown in Figure 3.3. High and low incident angle SAR returns were statistically similar for F2F and F5F descending pass sand and vegetation. The F1F and F4F ascending pass sand estimates were more similar to each other (Scheffe ascending p = 0.01) than to all other pair wise combinations (p = 0.000). The F1F and F4F ascending pass vegetation $\sigma°$ was different from all other pair wise combinations (each p = 0.000).

Table 3.2. Within class differences in backscatter by look and incidence angle for fine beam RADARSAT data. asc = ascending orbit; desc = descending orbit.

Statistic	Class	Study Area	Look Direction	Incident Angle	n	P value	Different? (P<0.05)
Anova	rock	1 + 2	asc + desc	all (F2N excl.)	116	0.242	no
Anova	sand	1	asc + desc	all	196	0.000	yes
Scheffe	sand	1	desc	F2F, F5F	196	0.761	no
Scheffe	sand	1	asc	F1F, F4F	196	0.010	yes
Anova	veg.	1	asc + desc	all	263	0.000	yes
Scheffe	veg.	1	desc	F2F, F5F	263	0.891	no
Scheffe	veg.	1	asc	F1F, F4F	263	0.000	yes

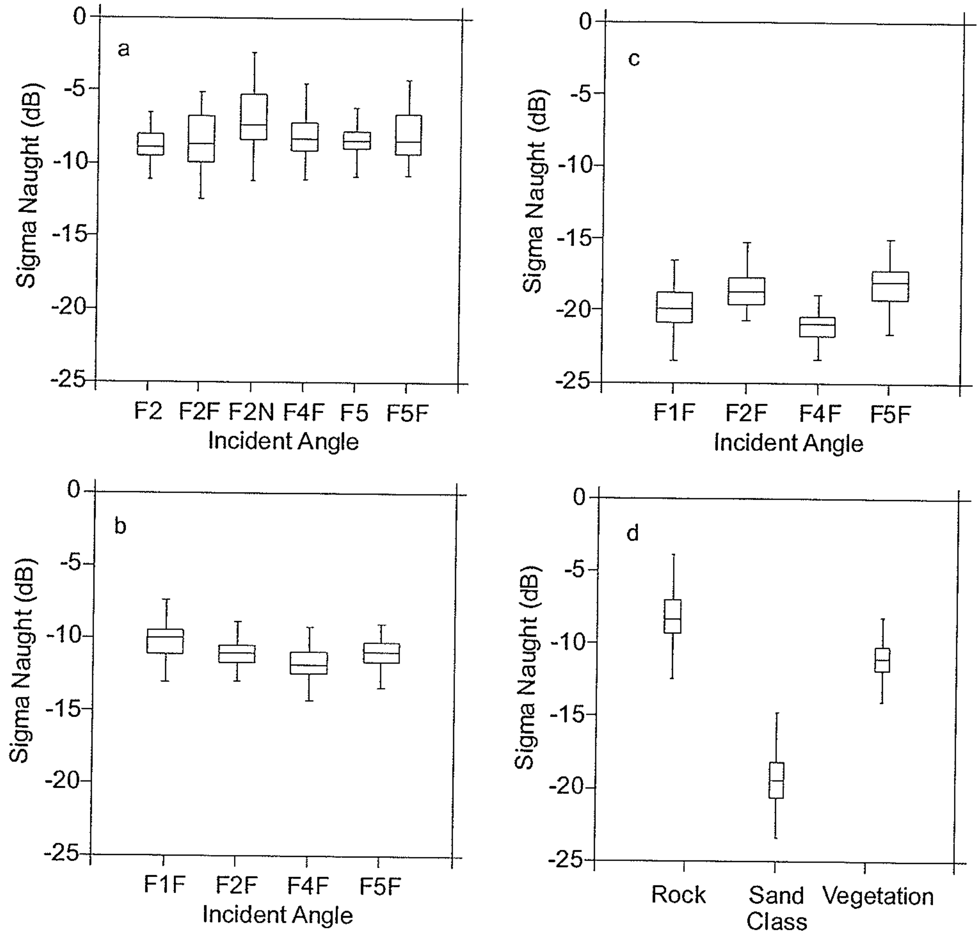

Figure 3.3. SAR backscatter for high and low incident angles for rock (a), vegetation (b), sand (c) shores. All rock returns are statistically similar, except for F2N (excluded due to unequal variance).

Backscatter derived from different incident angle and look direction for rock coasts was similar for all images tested. The F2N descending data were excluded due to unequal variance. While further statistical interpretation of the F2N data must proceed with caution, it is notable that the F2N data was only different from F2 ascending (i.e. the highest and lowest rock $\sigma°$ observed). To better understand within-class differences observed using ANOVA and the high F2N SAR returns on rock coasts, $\sigma°$ is reviewed with respect to shoreline declination, antecedent precipitation, and SAR calibration.

The angle of the rocky coast influences the magnitude of radar returns received by the SAR (Figure 3.4). Backscatter averages show that shoreline segments closer to the optimal viewing geometry at 90° tend to have higher σ° than those at the extremes of declination. The elevated σ° of the F2N image was investigated using a Geographic Information System. High σ° resulted mostly from two reaches of shoreline, about 700 m long in total. These coasts were approximately perpendicular to the look direction and provided high σ° averages (most pixels range -2 to - 5 dB) compared to other shoreline segments (most pixels range -4 to -9 dB).

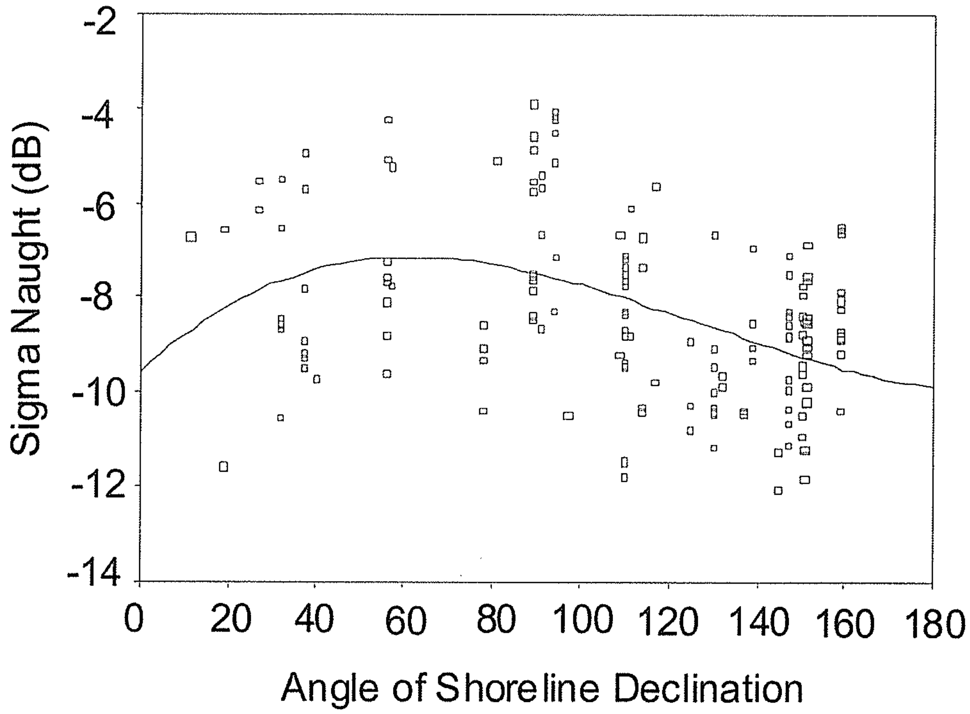

Figure 3.4. SAR backscatter values plotted by angle of shoreline declination for rock shores in both study areas. Optimal illumination geometry occurs when the shoreline aligns at ninety degrees from the satellite look direction.

Antecedent precipitation appears to elevate the average σ° (Table 3.3). For the 24 hour period prior to image capture, the F4F ascending image captured had negligible rainfall and shows the lowest σ° for sand and vegetation. The F2F and F5F descending images had similar amounts of rain and also had similar SAR returns. Boulder coasts may evaporate precipitation more quickly than sand or vegetated coasts, and so ascending (day) images are less likely to be sensitive to antecedent rain events than are the descending (night) images. The effect of optimal viewing geometry and rain combined appears to have contributed to the elevated σ° of the F2N descending image, and the only case of unequal variance in this study.

Table 3.3. Amounts of antecedent precipitation (mm) and the number of hours prior to capture for each radar image. Ascending images were captured during the day, descending at night. The * symbol denotes radar shadow.

Study Area	Beam Mode	Orbit	Mean Backscatter Rock	Sand	Vegetation	Antecedent Precip. (mm)	Hours Prior
1	F2F	Desc	-8.6	-18.4	-11.2	17, 14	12, 20
1	F5F	Desc	-8	-18.1	-11	31	21
1	F4F	Asc	*	-20.9	-11.8	0.4	11
1	F1F	Asc	*	-19.9	-10.2	14	3
2	F5	Asc	-8.3	-	-	5	3
2	F 2	Asc	-8.9	-	-	0	0
2	F2N	Desc	-6.9	-	-	1.4	2
2	F4F	Desc	-7.9	-	-	15	20

The interpretation of coastal RADARSAT data can sometimes be difficult due to sensor calibration issues resulting from the high contrasts evident between land and water (Vachon et al. 1997). As described by Gray et al. (1997), RADARSAT 1 uses an automatic gain control (AGC) to dynamically adjust the receiver gain. The AGC for an image is based on the signal power level in the near half portion of the image swath. If water is found in the near range and land in the far range, sensor saturation may occur because the gain is set too high for land. The reverse situation may occur if land is in the near range and water in the far range. This gain setting for land may produce AGC underflow in the far range. Vachon et al. (1997) determined the power loss over the coast and land was in the range of about 1.5 - 2 dB. For these data, the descending data for area 1 and all data of area 2 could be candidates for saturation. Underflow could occur for the ascending data of area 1. If saturation was present, I would expect for area 1 the associated loss of power would provide consistently lower σ° for the descending data, which is not the case. There was no visual evidence of AGC saturation in the images obtained for Lake Malawi. The present data more closely resemble the trend in amount of antecedent precipitation, particularly for the descending sand data captured at night.

Differences in σ° due to look direction, incident angle, or rain, are small relative to the range in σ° observed among classes, and fall within the 2 dB calibration range cited by Vachon et al. (1997). This supports pooling of σ° by class among images for the ANOVA because differences were about equal or less than known sensor calibration limits. The effects of rain on SAR σ° may be more clear in future coastal studies because calibration considerations can be limited by use of a fixed AGC setting (D. Wilson 2000 pers. com).

All data for each class was pooled, except for F2N, as differences observed within look or incident angle were within known sensor calibration limits (i.e. about 2 dB) for RADARSAT coastal studies (see Gray et al. 1997). ANOVA determined a difference between classes (ANOVA; P= 0.000, F = 2099.2, n = 575). Pair wise comparisons confirm that rock, sand, and vegetated SAR image tone are significantly different (Scheffe, each class P = 0.000) (Figure 3.3, inset d). Therefore, RADARSAT fine beam image data of varied look and incident angle data can be used as spatially adjacent data sources to separate homogenous rock, sand, and vegetated coastal zones.

3.3.3 Multivariate Discrimination and Classification

3.3.3.1 SAR

MDA of the classes using $\sigma°$ averages, declination, and slope data provided excellent separation of the groups (n=206) (Figure 3.5). An understanding of the relative importance of the variables in discrimination can be gained by examining the standardized canonical discriminant function coefficients (Table 3.4). The absolute values of the coefficients indicate the relative contribution of a particular variable to the discriminant axis. The first discriminant axis is the linear combination of the variables that best discriminates among the three apriori defined classes. This axis describes 80.4% of the variance in the radiometric and geometric data, and is dominated by $\sigma°$, with approximately equal loadings from shoreline declination and slope. The second discriminant axis is dominated by slope.

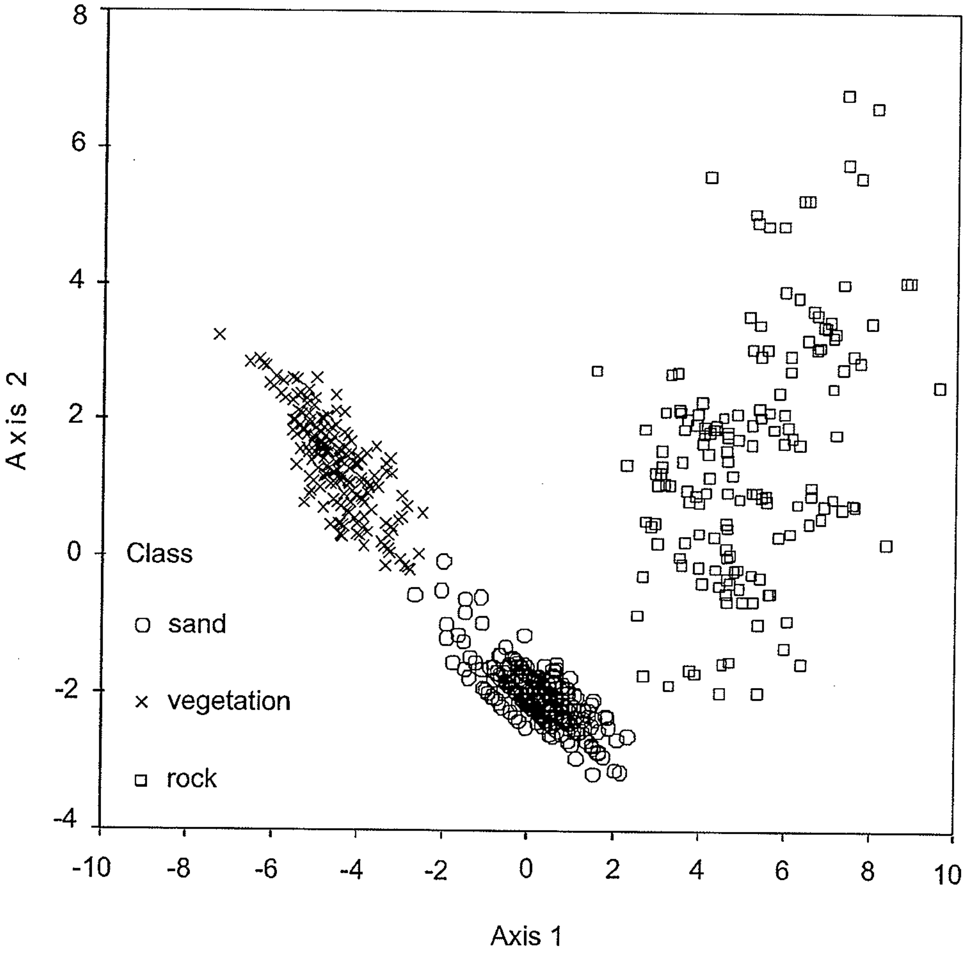

Figure 3.5. LDA separation of rock, sand, and vegetation using radiometric (SAR backscatter) and geometric variables (coastal slope and the shoreline angle of declination). Axis 1 is dominated by SAR backscatter. Axis 2 is dominated by coastal slope.

Table 3.4. Standardized discriminant function coefficients derived from 8 RADARSAT images containing rock, sand, and vegetation.

Discriminant Axis	1	2
SAR (F2N - F5F)	0.826	-0.512
Declination	0.534	0.004
slope	0.516	0.865
% variance	80.4	19.6

3.3.3.2 *RADARSAT and SPOT*

It can be shown that Pearson correlation coefficients for each class are significant between the F5F and F2F descending SAR images for rock, sand, and vegetation. For the SPOT data, spectrally adjacent image bands contain redundancy in information. Correlation is high and positive between bands 1 - 2, and between 3 – 4, and negative for correlation between the visible and infrared bands. In general, the higher the correlation among pairs of variables, the less likely the correlated pairs of variables will improve discrimination.

MDA of the SPOT data provided a weaker discrimination than the SAR (Table 3.5). Bands 2 and 3 contributed most to axis 1, with a small contribution by band 1. Bands 1 and 2 with very similar weights dominated the second discriminant axis. The equal loading from band 1 and 2 would be expected. Within-class correlation among these bands is significant, indicating similar class reflectance.

Table 3.5. Standardized discriminant function coefficients derived from RADARSAT and SPOT images containing rock, sand, and vegetation.

	SPOT		SAR F2 + SPOT		SAR F2 F5F + SPOT	
Discriminant Axis	1	2	1	2	1	2
SAR F2 Sigma			1.019	0.144	0.574	0.365
SAR F5F Sigma			-	-	0.578	-0.214
Band 1	-0.499	-2.89	0.552	0.065	0.121	0.256
Band 2	1.66	2.95	-0.254	1.128	0.263	0.895
Band 3	-1.13	0.908	-0.224	-1.312	-0.086	-1.345
Band 4	-0.13	-0.274	-0.057	0.167	-0.193	0.21
% variance	75	25	78.1	21.9	80.5	19.5

Discriminant axis 1 for SPOT primarily separates vegetation from rock and sand. Vegetation reflectance in band 2 is low and provides the best separation from the others because sand and vegetation have a similar reflectance in band 3. Discriminant axis 2 best separates rock from sand and vegetation. In bands 2 and 1, reflectance of vegetation is low, but is relatively high for sand. The contribution of band 3 to discriminant axis 2 appears to separate the low reflectance values of rock from the higher and similar sand and vegetation values.

SAR F2 and SPOT improved class discrimination by use of the dominant variables observed in the first canonical axis determined in the MDA for SAR and also for SPOT. The dominant trend of the combined SAR and optical data was provided by SAR F2 that weighted the first axis most, with a smaller contribution from SPOT band 1. Discriminant axis 2, like axis 1 for the SPOT MDA, was weighted most by SPOT bands 2 and 3 demonstrating the use of the dominant trend in the optical data (i.e. separation of vegetation and sand). Due to the correlation of SAR data, the combination of SPOT, SAR F2, and SAR F5F only marginally improved discrimination. The correlated variables can be observed as equal weights in the discriminant function. Bands 1 and 2 are not well correlated with band 3, but are correlated with SAR for rock and vegetation. Thus, band 1 contributes to the first discriminant axis dominated by SAR. The combination of SAR and SPOT data within a single discriminant axis is determined by the relative amount of correlation of each variable to the dominant variable(s) of that axis. Given that the data from each of these platforms is complementary but very different, the within-axis correlations among SAR and SPOT need not have direct interpretation.

3.3.3.3 Classification Agreement

Classification agreement for the Model and Test shoreline segments to which class membership was predicted for the SAR and SAR + SPOT is shown in Table 3.6. Cross validation results for the test groups were only marginally lower (<1.2 %) than for the model groups, except for the SPOT data. In general, this suggests the sample size (33%) for the Model groups are sufficiently large and represent the full range of multivariate data. The overall agreement in classification of the SAR Test group is excellent, at 98.3%. Agreement between predicted and validated SAR classes showed 95.2% for rock, 100 % agreement for sand, and 98.9% for vegetation. Vegetation was only miss-classified as sand, and rock was only miss-classified as vegetation.

Table 3.6. Classification agreement (%) for fine beam RADARSAT backscatter and SPOT reflectance averages from shoreline segments 150 meters in length.

LDA Variables	Number of Variables	Model Agreement (%)	Test Agreement (%)	Rock	Test Sand	Vegetation	Test Total Shore Segments
SAR, slope, declination	3	99.1	98.3	95.2	100	98.9	400
SPOT	4	93.2	79.3	90.9	75.8	79.1	87
SAR F2, SPOT	5	100	98.9	100	100	97.7	87
SAR F2, F5F, SPOT	6	100	98.9	100	100	97.7	87

The reduction in overall classification agreement of the SPOT Test data was due to lower classification agreement in all three Test classes (9 -15% reduction). Recall that optical and SAR data are available only in area 1. This suggests the smaller number of shoreline segments used to develop the discriminant model in area 1 (n = 44) is inadequate to represent the range of data for the Test group. The reflectance averages for each shoreline segment vary more than those derived from SAR due to larger pixel size (smaller sample number), and also because of a few mixed pixels along the coastal boundaries. While improving discrimination and achieving a high classification agreement, the combination of data from optical and more than one SAR image does not improve classification agreement.

3.4 Conclusions

The objectives of chapter 3 were to: 1) Assess the effects of incident angle and look direction on SAR backscatter for each class. 2) Assess if SAR backscatter can be used to effectively discriminate and classify rock, sand, and vegetated coasts. 3) Assess the merit of combining SAR + SPOT to evaluate an entirely remote approach to discrimination and classification.

Objective 1 was addressed in the section called "univariate analysis of SAR backscatter". Only rocky coasts are suspect for radar shadow and imaging of the rock coast is best when the look direction faces the shoreline. It was shown that incidence angle had no effect on the σ° from the descending (night) pass for sand and vegetation, and that the ascending (day) scattering was lower than at night and this was most notable for sand. This probably is attributed to diurnal changes in moisture due to rain at night, and percolation/evaporation from the beach during the day, but quantitative observation is merited.

Within a look direction, incident angle has no effect on the magnitude of σ° on rock coasts, but the angle of declination and rain appears to influence the magnitude of scattering. A single image was wetted by rain just prior to image capture and showed the highest returns of all rock samples and was the only image with a different variance structure. It was shown that although the scattering of microwaves from a rock coast is complex and results in a wide range of σ°, a clear pattern emerges where σ° tends to be strongest when the viewing geometry is optimal.

Rock, sand, and vegetated image tones unaffected by recent rain are within known sensor limits and are significantly different. This provides strong evidence in support of coastal discrimination using SAR backscatter.

Objectives 2 and 3 were addressed in the section named "multivariate discrimination and classification". The SAR data were first treated independently, then compared to RADARSAT and SPOT. It was shown that RADARSAT fine beam data was the strongest discriminator between rock, sand, and vegetation in this study. Interestingly, when SAR and SPOT data are combined the process of ordination essentially extracts the first discriminant axis obtained in the SAR and of the SPOT trial. This demonstrates that SAR and optical data are mostly uncorrelated and so are complementary.

The results of the coastal classifications using the two independent or combined data sources was, in general, excellent. SAR coastal classification using fine beam data was complicated most by the relatively abundant low dB SAR returns, characteristic of forward scattering away from the SAR instrument, in all three classes. The prevalence of low dB signals was shown for raw pixel data, was evident as long-tails in the pixel frequency distributions, and low dB returns were detected most frequently in the adaptive filter trials. Further, because rock was only miss-classified as vegetation, and vegetation was only incorrectly classified as sand, low dB returns appear to be a principal source of error in classification.

In summary, RADARSAT SGX data have demonstrated excellent potential for discriminating rock, sand, and vegetated coastal attributes. The main operational challenge for the use of RADARSAT-1 data to classify the coast of Lake Malawi is the requirement for highly precise positioning of all image data due to the narrow extent of the coast. Numerous GPS surveys would be essential in each of the many image areas that would be required to map the lake. This is not a realistic expectation and would take longer than direct aerial observation. Therefore, the use of an aerial approach merited investigation and is provided in the next chapter.

Chapter 4 The Coastal Zone of Lake Malawi, Africa: a geographic framework for allopatric divergence

4.1 Introduction

In this chapter, I study the distribution and scale of fish habitat surrounding Lake Malawi at regional and local scales and attempt to assess the validity of a major low lake stand reported to have occurred between 150 and 500 years ago. A focus of the chapter is to describe the habitat distributions at current lake level. However, the study of a recent low lake stand site is needed also to weigh the relative importance of habitat distributions observed at current water levels against those that may have influenced fish distributions at lower water levels, in evolutionary terms, in the very recent past. From these two standpoints it becomes clear that the primary focus of this chapter is to develop an understanding of how the tectonic framework of the Malawi Rift basin controls the availability of fish habitat. Once these objectives have been completed, this chapter then makes the first comparison between the habitat distributions to recently published mbuna (i.e. rock dwelling cichlids) species distributions at the regional scale. A study of this type has previously never been done at Lake Malawi because the habitats have not received directed study, leaving the expression of landform on habitat availability unstudied. Additionally, the first publication of regional species distributions at the lake wide scale for the mbuna was only a few months in advance of this writing.

Understanding the linkage between the distribution of physical habitat and species distributions provides novel information to enable the development of conservation strategies based on the more readily observed habitat distributions, and the available species data. In essence, the approach under evaluation in this chapter and dissertation is to determine if habitat boundaries, i.e. changes in substratum composition over space and depth, can be used as ecologically meaningful boundaries for parks/mangement units. If so, such strategies would not be pre-empted by an incomplete understanding of the distribution of all 845+ species (Snoeks 2000) which, at present, is far from complete. Information on the distribution and size of habitats discontinuities could also provide new insights about the role of allopatry in the basin. The objectives of this chapter are:

1) *Relate the distribution and composition of the coastal zone to the tectonic setting.*
2) *Assess the scale of coastal habitat discontinuities by comparing the size (i.e. length and depth) of the main coastal types according to landform.*
3) *Validate the character of a site described in the literature as a low lake stand 120 m below present.*
4) *Show the influence of the tectonic structure of the Malawi Rift on the regional distribution of species composition.*

4.2 Methods

4.2.1 Lake Wide Coastal Data

The study areas are shown in Figure 4.1. The first aerial video frame surveys of the coastal zone of Lake Malawi were undertaken during the low water period on December 7 and 8, 1998 from 800 – 940 MSL (water level 474 MSL). All image data were captured using oblique viewing directions taken within the six seat Cessna aircraft using a Sony Hi8 Handicam (CCDTRV72 NTSC). The video frame surveys proceeded over water in a clock-wise direction beginning at Senga Bay in a northerly direction, circumnavigating the lake using the angle of the sun to illuminate the coast. Most frames were captured without magnification at a direction approximately perpendicular to the coast. A differential global positioning system was affixed to the aircraft and logged sub-meter position and time stamp data at 1-second intervals. The surveys are described in detail by Cooley (1998).

Figure 4.1. Study areas of the coastal and littoral habitat mapping (inset).

The coast was defined as starting at the water level on the date of survey to not more than about 150 meters from the waters edge, where change to terrestrial areas were easily noted, except for wetlands. The coast was interpreted visually into one of eight classes: 1) Rock, 2) Sand, 3) Vegetation, 4) Sand/Vegetation, 5) Rock/Sand/Vegetation, 6) Rock/Sand, 7) Gravel, and 8) Rock/Vegetation. The coast was interpreted for segments greater than 50 meters long. Coastal boundaries were identified and mapped using the time stamp that was common to the video and GPS data. Error in positioning of boundaries is expected to be less than 20 m.

A terrestrial and aquatic digital elevation model for the Lake Malawi watershed was assembled at 1 kilometer resolution using a GTOPO30 data. Elevation for Lake Malawi was interpolated to the same grid using 20 m contour information (Cooley et al. 1998) drafted by project PROBE (Johnson and Halfman 1987). A map of percent slope was derived from the DEM using the method of Eastman (1999). The mean slope of the terrestrial and aquatic for each segment of coast was derived using a 3 km distance buffer on each side of the shoreline.

The shoreline of Lake Malawi was classified into rift scarp and lakeshore plain geomorphologic classes (Cooley et al. 2003) consistent with maps of geomorphology for Malawi at 1: 100000 scale (Malawi 1986). The lakeshore plain class represents the Rift Valley floor and was subdivided into erosion and deposition classes. Erosional relief represents dissected low-altitude plains, piedmont zones, and raised beach remnants, with varying slopes. Depositional relief consists of nearly level land formed by alluvium brought down from the scarp zones. The coastal zone also was classified according to rift structures according to Crossley (1984), Specht and Rosendahl (1989) and Owen and Crossley (1989). A RESURS 01 multispectral satellite image captured on October 24 1998 (170 m resolution) was interpreted to classify the coastal geomorphology of Mozambique and Tanzania, and to precisely locate the extents of rift structures.

4.2.2 *Statistical Analyses*

To better understand how the composition of the coast is influenced by landform (i.e. geomorphology and slope), Correspondence Analysis was used to test if response probabilities varied between these two factors across each coastal category. This is a graphical technique that demonstrates which rows or columns of a frequency table have similar patterns of counts. The technique is particularly useful for tables with many levels (Sall et al. 2001), in this case three geomorphologic regions, three levels of slope, and eight levels of coastal type. Slope classes were identified with class limits at 4 and 8 % by visual inspection of a frequency histogram. Multiple Correspondence Analysis (Wilkinson 1989) was used to present the data in a single figure as the position and pattern of treatments was the same as in the bivariate plots. All correspondence analysis statistics were produced using using JMP.IN software (Sall et al. 2001).

Differences in the length of coastal types by geomorphologic class was determined using the Kruskall-Wallace and Wilcoxon statistical tests. Kruskall-Wallace tests were not undertaken for gravel, rock/sand/vegetation, and rock vegetation due to small sample size. Similarly, Wilcoxon pair wise tests excluded comparisons for vegetation in rift scarps. Coastal toponymy is consistent with Konings (2001).

4.2.3 Littoral Data

Information on the observed depth of the rock/sand boundary was compiled for 150 sites distributed around the lake from Ribbink et al. (1983), Spreinat (1995), and from the SCUBA logs of Ad Konings. In the case of Konings, where a range was provided the maximum was chosen. The low lake stands reported by Owen et al. (1990) at Domwe Island were studied using a vertical beam sonar system coupled to a sub-meter GPS, as described in Chapter 5.

4.3 Results and Discussion

4.3.1 The Tectonic Framework, Geomorphology, and Coastal Habitat

The lakeshore plain is the major geomorphologic feature bounding Lake Malawi (Figure 4.2). This class represents 1424 km (85%) of the lake coastline, of which 876 km (52.3%) is depositional relief and the remaining 548 km (32.8%) is erosional relief. Despite being an obvious and majestic feature of the lake, rift scarps form only about 250 km (15%) of coastline. Four of the eight types of coast (Figure 4.3 – 4.5) total 91% of the coast of Lake Malawi (Table 4.1). Of this fraction, sand and sand/vegetation total 59% of the coast. Rock shores are the second most abundant class and are second only to sand beaches. The mixed classes are rare and total 9%.

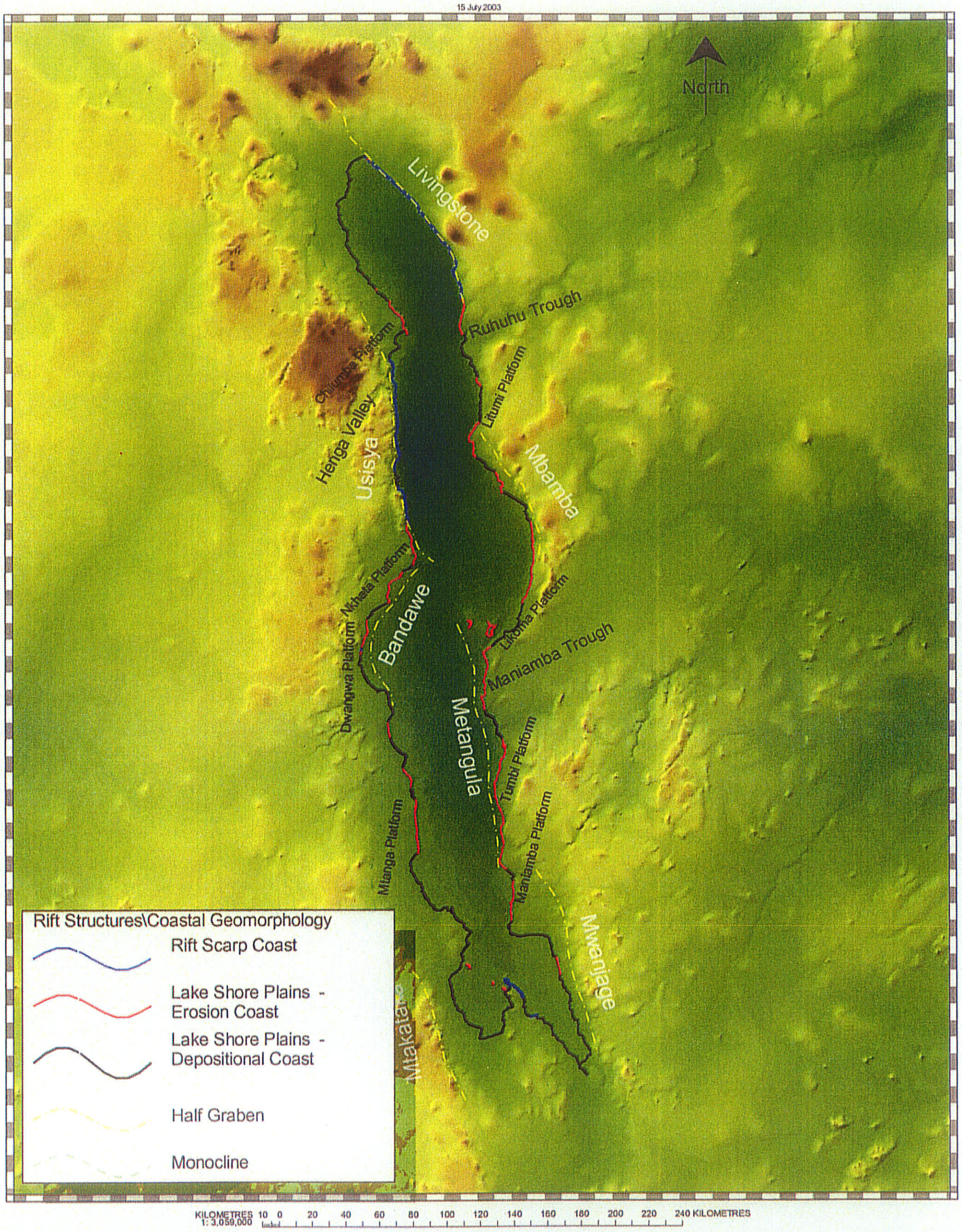

Figure 4.2. Geomorphologic classification of the coastal zone of Lake Malawi. Rift structures adapted from Crossley (1984), Specht and Rosendahl (1988) and Owen and Crossley (1989). The half grabens represented by yellow lines represent border faults.

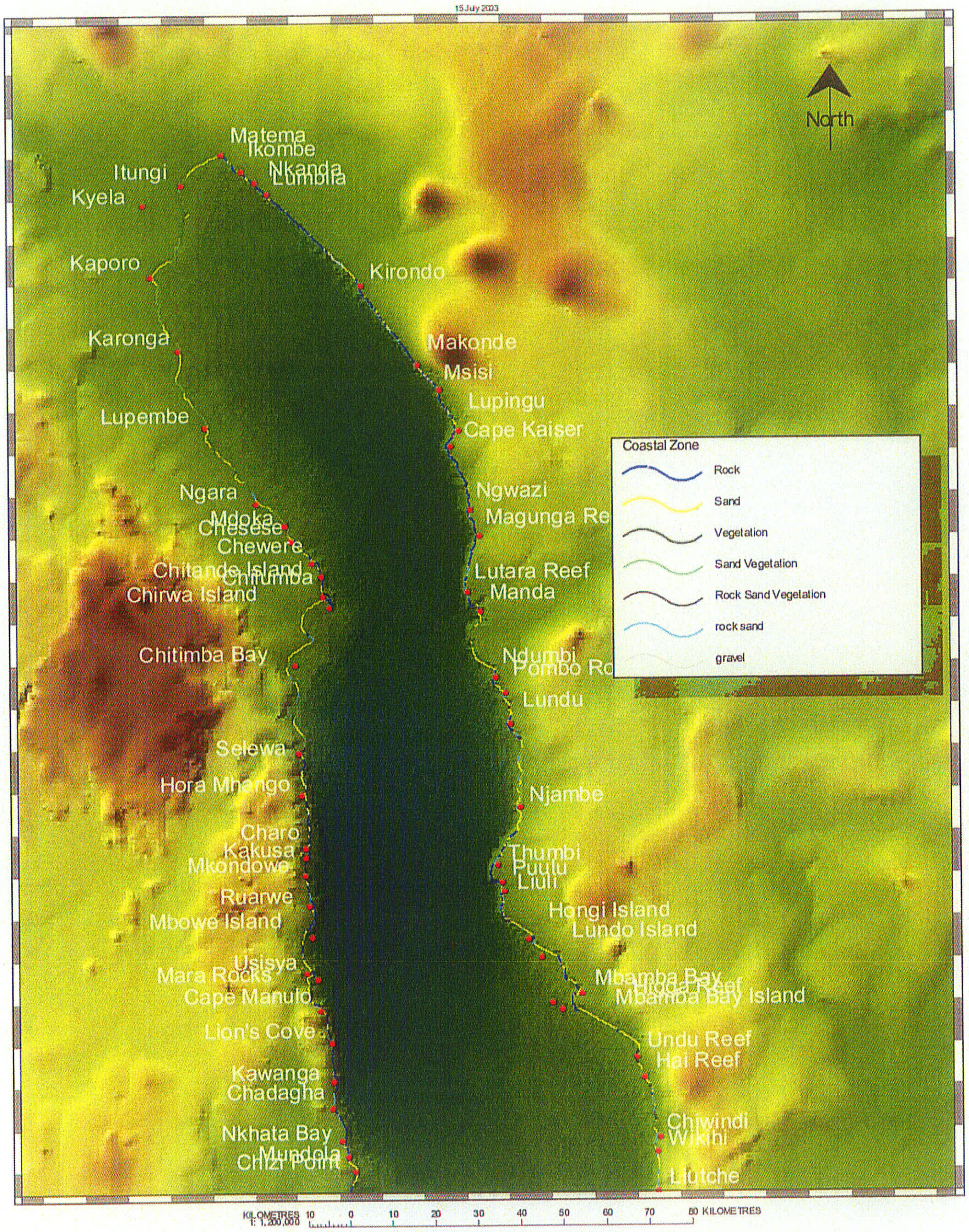

Figure 4.3. The coastal zone of the northern region of Lake Malawi. Toponymy from Konings (2001). Adapted from Cooley et al. 2003.

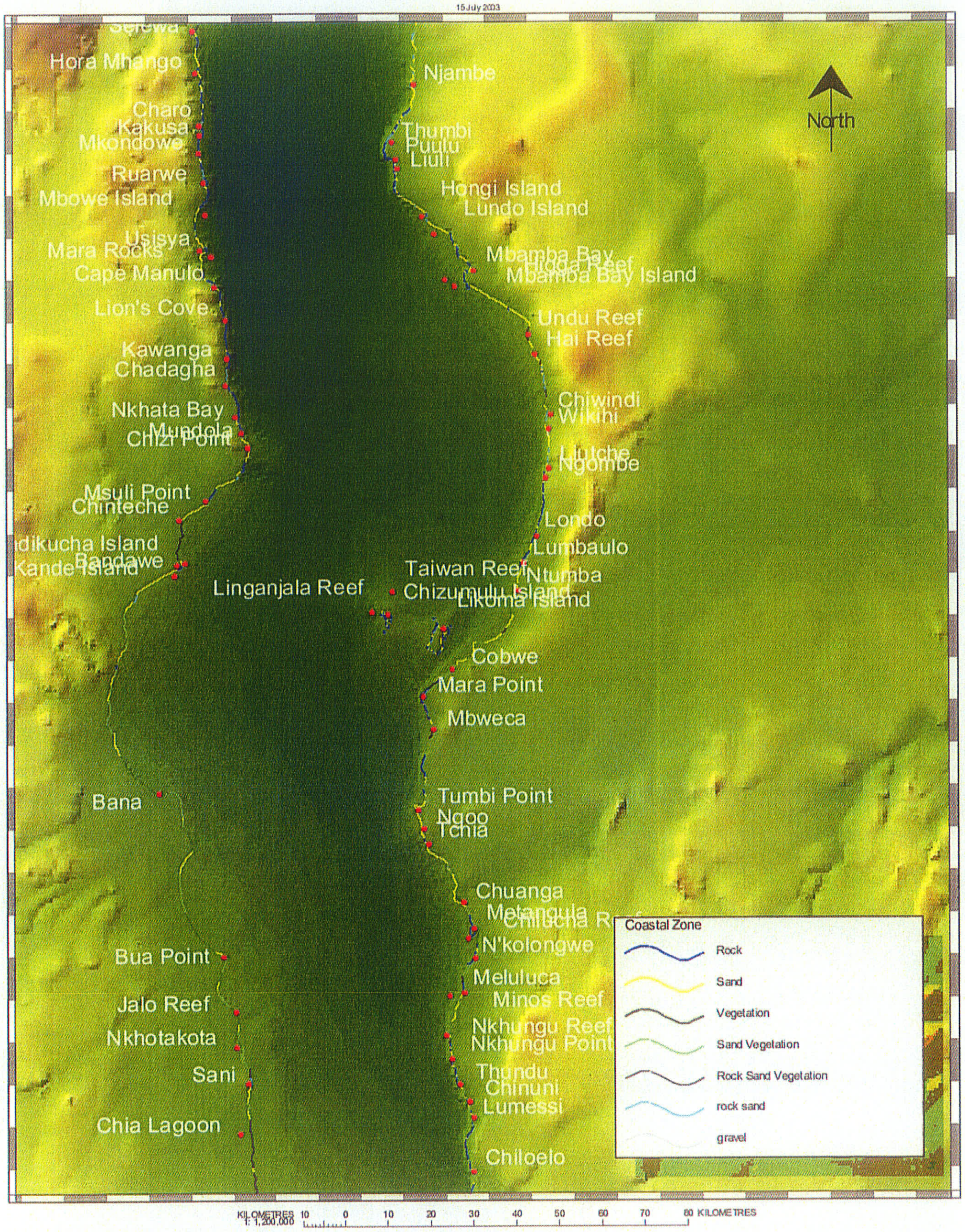

Figure 4.4. The coastal zone of the central region of Lake Malawi. Toponymy from Konings (2001). Adapted from Cooley et al. 2003.

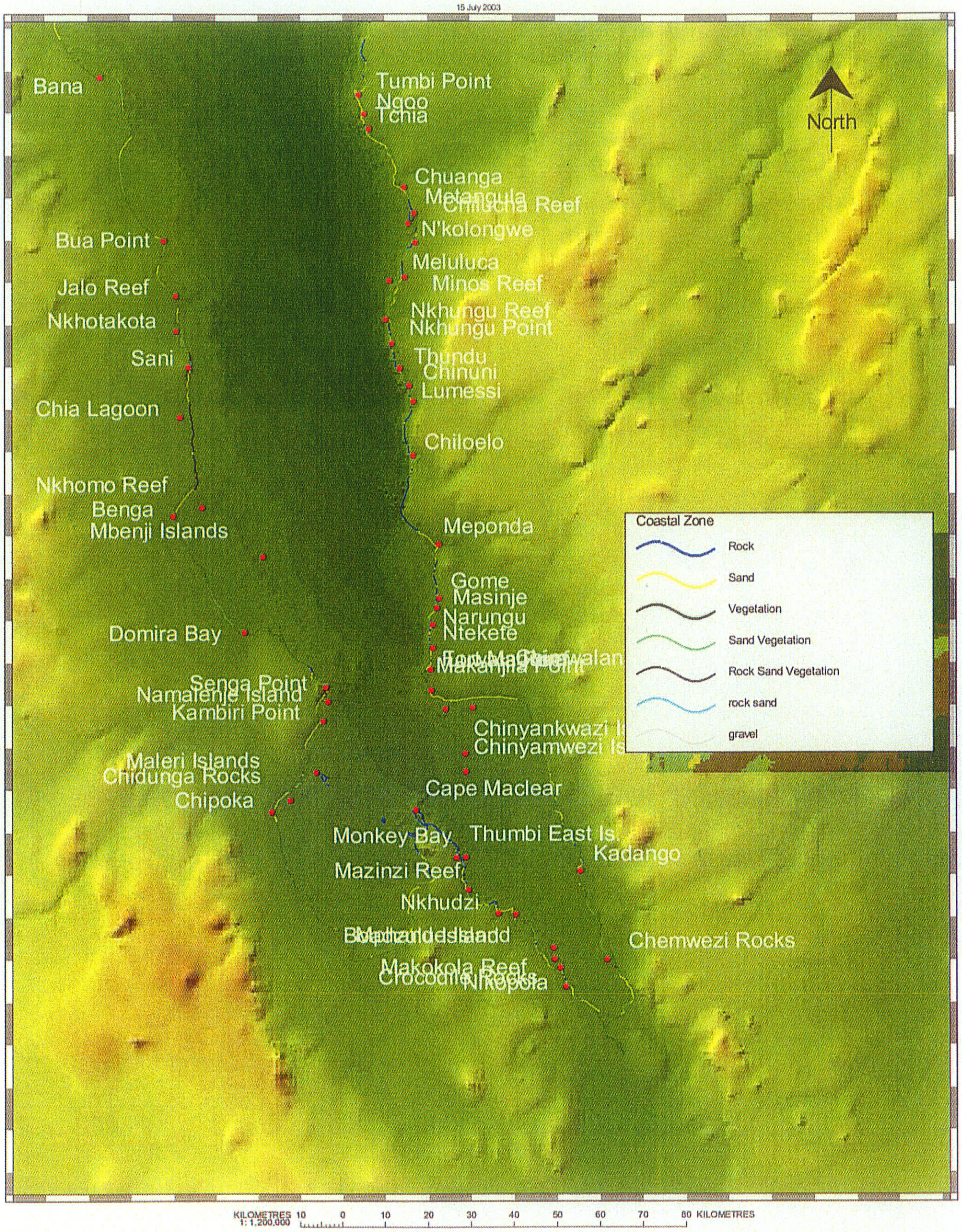

Figure 4.5. The coastal zone of the southern region of Lake Malawi. Toponymy from Konings (2001). Adapted from Cooley et al. 2003.

Table 4.1. Total shore length (km) for eight classes of coast for Lake Malawi at 474 msl.

Class	Shorelength (km)	Percent
Sand	559.6	33.4
Rock	434.0	25.9
Vegetation	302.8	18.1
Sand/Vegetation	236.3	14.1
Rock/Sand/Vegetation	54.3	3.2
Rock/Sand	51.2	3.1
Gravel	23.4	1.4
Rock/Vegetation	12.5	0.7
Total	1674.2	100

There are clear associations between the type of coast, the geomorphology, and the slope of the coastal zone. The Correspondence Analysis shows that this association is highly significant for geomorphology and slope (inertia = 99.9%. X^2 = 299.9, P<0.0001, inertia = 99.9%, X^2 = 482.5, P<0.0001), respectively. The inertia value represents a measure of the amount of variation accounted for by the canonical dimensions (Sall et al 2001). A high proportion means that high confidence can be placed on the 2 dimensional plot as it is a good approximation of higher dimensional relationships in the data.

The correspondence plot shows clearly the intuitive relationships among the type of coast, regional geomorphology, and coastal zone slope (Figure 4.6). The left side of the plot represents rocky coasts in an erosional or rift scarp setting with moderately high slope (4 - 8%). The right side represents a coast where vegetation is found in depositional areas with slope less than about 4%. Mixed classes (e.g. rock/vegetation and rock/sand/vegetation) represent heterogeneous coasts that correspond to erosional relief. The strength of the association in this plot increases with axis length. In the case of rock/vegetation and gravel the correspondence with the other variables is high because these classes are rare and unique to erosional or rift scarp relief, respectively. In contrast, vegetation is abundant and also demonstrates a strong correspondence.

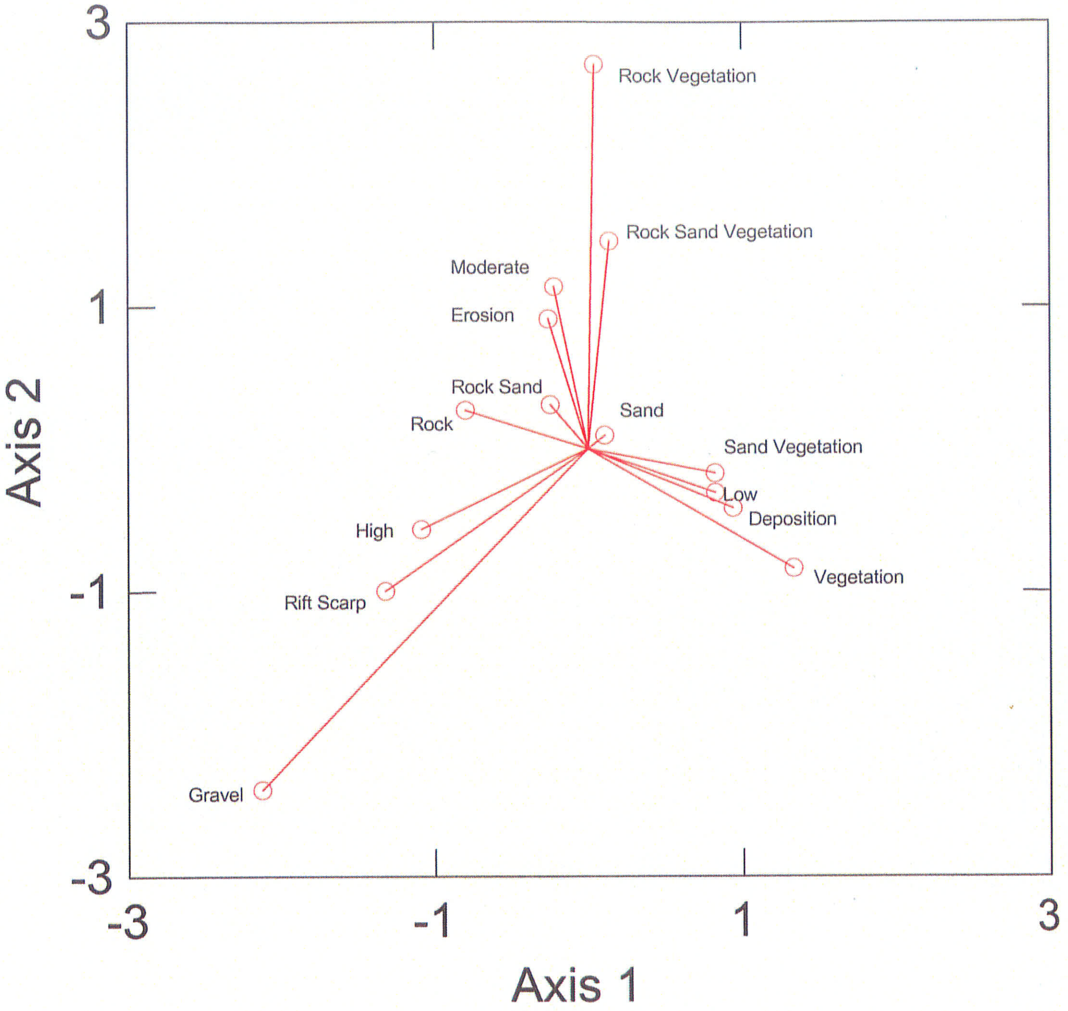

Figure 4.6. Multiple Correspondence Analysis plot of geomorphologic classes (rift scarp, erosion, deposition), coastal zone slope (high, moderate, low) each within 3 kilometers of the coast, and their relationship to eight shoreline classes for all of Lake Malawi.

The associations demonstrated by the correspondence plot are evident also in the observed coastal data (Table 4.2). Erosional relief and rift scarps represent nearly all homogeneous rock coasts (93%), as well as many areas that contain rock. The depositional areas of the lakeshore plains represent 67% of homogenous sand coasts and

94% of homogenous vegetated coasts. Sand, however, is more central in the correspondence plot than is vegetation and does not group with the low slope and deposition categories. This is due to the fact that sand coasts are relatively ubiquitous; about one-third (33%) of sand coasts are found also in erosional and rift scarp landforms. Beaches in erosional relief are typically small, crescent shaped, and are located between rocky headlands, or separate relatively long sections of rocky coast. In contrast, along rift scarps many sandy areas are small river deltas formed by alluvial deposits. More than 90% of the gravel coasts were observed adjacent to rift scarps.

Table 4.2. Total length of coast (km) tabulated by geomorphologic class (deposition, erosion, and rift scarp) for 8 types of coast.

Geomorphology	Coastal Class								
	Gravel	Rock	Rock/Sand	Rock/Sand/ Vegetation	Rock/ Vegetation	Sand	Sand/ Vegetation	Vegetation	Total
Deposition (km)		29.4	18.3	6.4		375.6	161.5	284.9	876.1
Erosion (km)	2.2	246.6	27.2	46.7	12.5	134.5	62.9	15.8	548.4
Rift Scarp (km)	21.3	158.0	5.6	1.1		49.6	11.9	2.1	249.7
Total (km)	23.4	434.0	51.2	54.3	12.5	559.6	236.3	302.8	1674.2

The slope of the coastal zone is significantly different among landform types (Kruskall-Wallis, $X^2 = 300.4$, $P<0.0001$), providing evidence for regional differences in character of the coast (Figure 4.7). Pair wise comparisons confirm the slope of each class is statistically different (Table 4.3). The average slope of the deposition, erosion, and rift scarps are 3.1%, 6.1%, 11.2%, respectively.

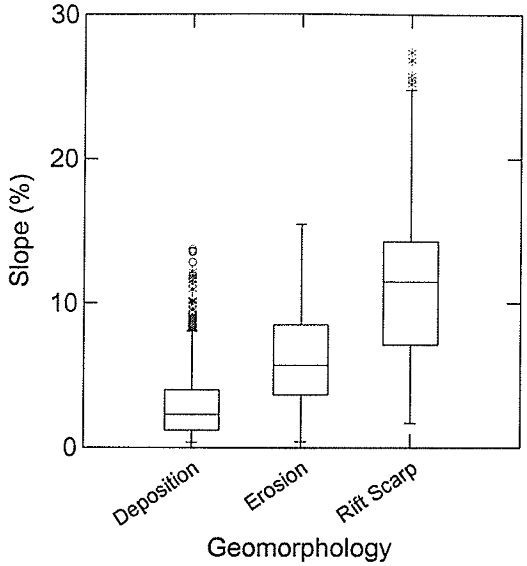

Figure 4.7. Percent slope box plots for three geomorphologic classes showing mean slope, the 25th and 75th percentiles and 95% confidence limits.

Table 4.3. Wilcoxon test pair wise comparisons determine that the center of the slope distributions for 3 geomorphologic classes are not equal for the coastal zone of Lake Malawi.

Wilcoxon	z	P
Rift Scarp vs. Depositional	19.96	<0.0001
Rift Scarp vs Erosional	12.89	<0.0001
Erosional vs. Depositional	-16.77	<0.0001

4.3.2 Habitat Discontinuities

The coastal geomorphology is a strong indicator of the predominant material types and also sets the scale and continuity of coastal habitat (Table 4.4). Discontinuities arise due to local conditions that change the availability of the regionally dominant material. For example, alternating sequences of rock and sand coastal habitat are common on rift scarps where incised river valleys are terminated by sandy deltas. The distance between such interruptions sets the scale of both the dominant, or major habitat, and the stretch of discontinuity, or minor habitat.

Table 4.4. Frequency and average length (km) statistics for the 8 types of coastal zone pooled by geomorphologic class in Lake Malawi.

Geomorphology		Coastal Class							
		Gravel	Rock	Rock/Sand	Rock/Sand/ Vegetation	Rock/ Vegetation	Sand	Sand/ Vegetation	Vegetation
Deposition	Frequency	-	26	15	6	-	118	66	60
	Average Length (km)	-	1.13	1.22	1.07	-	3.18	2.45	4.75
Erosion	Frequency	2	139	20	15	8	133	36	11
	Average Length (km)	1.09	1.77	1.36	3.11	1.56	1.01	1.75	1.43
Rift Scarp	Frequency	22	68	3	1	-	46	6	2
	Average Length (km)	0.97	2.32	1.88	1.11	-	1.08	1.99	1.07
Total Frequency		24	233	38	22	8	297	108	73

Statistical tests confirm the length of rock, sand, and vegetated coasts are each significantly different when compared by landform (Table 4.5), indicating the major and minor constituents of the coast can be inferred by the geomorphologic setting. Pair wise comparisons by class demonstrate that the length of coastal segments are significantly different across landforms, except for rock (deposition vs. erosion) and sand (rift scarp vs. erosion) (Table 4.6). The similarity in length of rock coasts may result given both classes reside in the lakeshore plains. The length of sand coasts is similar between rift scarp and erosional landforms as they both contain river deltas or cusp shaped and small (1 km long) beaches between headlands. Given that rock and sand are major habitat types this also reveals that erosional coasts have a greater diversity (i.e. number) of coastal types and so often have shorter segment lengths. Coasts of rock/sand/vegetation are rare but are most abundant on erosional coasts.

Table 4.5. Kruskal Wallace within-class tests of coastal segment length by geomorphologic class for the four main types of coast.

Class	x^2	P
Rock	10.915	0.004
Sand	57.889	<0.0001
Vegetation	7.065	0.029
Sand Vegetation	2.32	0.314

Table 4.6. Wilcoxon test comparing the length of rock, Sand, and Vegetated shores of Lake Malawi and geomorphologic classes.

Class	Pairwise Comparison	z	P
Rock	Rift scarp vs. Erosion	5.49	<0.0001
	Erosion vs. Deposition	-1.8	0.0714
	Deposition vs. Rift Scarp	-3.21	0.0013
Sand	Rift scarp vs. Erosion	0.071	0.9427
	Erosion vs. Deposition	-7.02	<0.0001
	Deposition vs. Rift Scarp	-5.28	<0.0001
Vegetation	Rift scarp vs. Erosion	-	-
	Erosion vs. Deposition	-2.45	0.0142
	Deposition vs. Rift Scarp	-	-

Sand/Vegetation coasts are not different in length among landforms. However, a clear trend of decreasing segment length and class frequency is evident from deposition to rift scarp. Sand therefore, represents a major habitat in depositional relief, but only rarely forms a large discontinuity in predominantly rocky coastal areas.

The maximum depth of the rock/sand boundary is very shallow for rocky areas in the depositional areas of the lakeshore plains, and is similar for rift scarp and erosional coasts with the frequently reported depth at about 35-40 m. The variability in the distribution of the recorded depths (Table 4.7) shows that deposition and rift scarp areas have a more uniform depth of the rock/sand interface than do erosional coasts.

Table 4.7 Select percentile depths (m) of the rock/sand boundary for deposition (n = 11), erosion (n = 104), and rift scarp (n = 30) coasts representing all coastal regions of Lake Malawi at the half graben scale.

Percentile	Deposition	Erosion	Rift Scarp
80	3	35	40
65	3	22	40
50	3	17	30

Changes in habitat availability due to water level variation can be inferred from habitat distributions at current lake level. In the depositional areas of the lakeshore plains the slope transition at the rock/sand interface is abrupt and yields extensive low slope sand platforms. Water level declines, using the current annual evaporative loss of 1.6 m (Patterson and Kachinjika 1995), suggests only a few consecutive years of declining lake levels will result in loss of many rocky habitats because the sand platforms characteristic of this region would result in rapid horizontal shoreline retreat; thereby preventing compensatory erosion of sand to rock. The variable depths to the rock/sand interface of erosional habitats, and smaller patch size with an intermediate but frequently variable slope, appears to correspond to the more variable shoreline configuration observed during the aerial surveys. In many erosional areas, cusp-shaped beaches form between headlands and show a range of littoral slopes. In other erosional areas rock is locally abundant and the shores appear more linear and have a higher littoral slope. The apparent effect of lake level variation in erosional topography would be variable with the low slope/curvilinear shores being more prone to desiccation and habitat loss. The temporal availability of the rift scarp littoral appears highest due to a combination of high slope, predominantly rock substratum that extends relatively deep, and wide exposure (frequently 180°) for wave energy to cleanse the substratum as lake levels fall.

The preceding suggests the temporal availability of the rock habitat ranks from high on rift scarps to low on depositional relief, at least during a steady state lake level condition. Accordingly, rock dwelling mbuna populations on rift scarp relief could shift up and down the rocky coast with small (<40 m) changes in water level with little consequence of landform to habitat availability. In contrast, lateral (i.e. involuntary) movement of the mbuna might be expected more frequently during periods of lake level variation on erosional rock habitats and due to smaller patch size and larger distances between patches. Extinction of mbuna probably would be most frequent in rock habitats found in the depositional areas of the lakeshore plains.

4.3.3 The 120 m Low Lake Stand

The low lake stand 120 m below present reported by Owen et al. (1990) just 500-150 yr before present has raised much controversy. To confirm the temporal persistence of and to reveal in more detail the spatial form of the feature, I mapped and validated the surficial composition of the substratum on the east side of Domwe Island (Figure 4.8), using sonar and ponar benthic samples. The methods are described in Chapter 5.

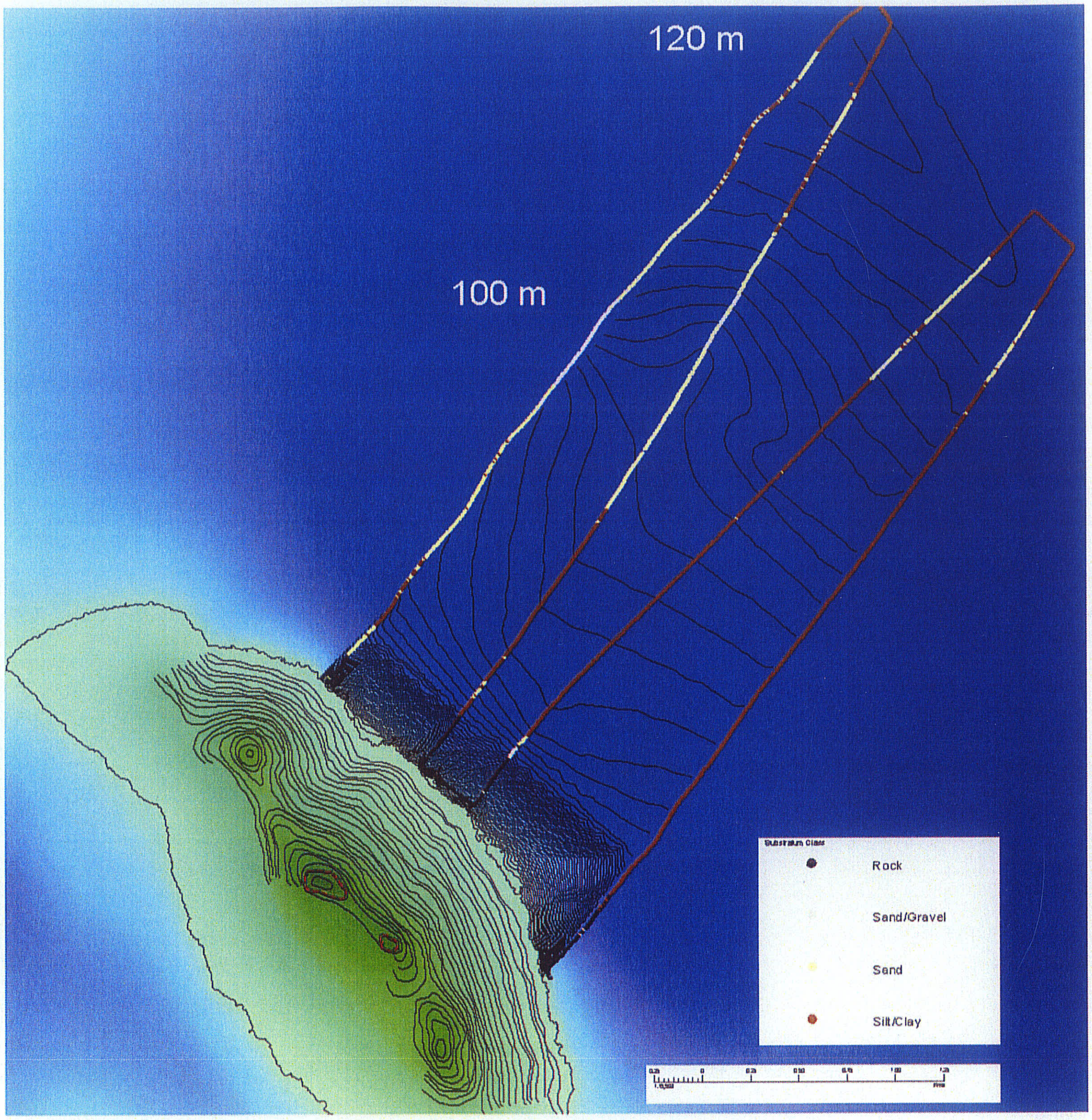

Figure 4.8. Depth and substratum for the eastern littoral of Domwe Island where Owen et al. (1990) noted erosional features at 120 m attributed to low lake stands. Contour interval is 2 m. n = 1847 sonar returns indicated as colored dots.

The features observed by Owen et al. (1990) are confirmed here. The erosional features reported as "hard reflectors" are apparent in the form of gravel bars at 100 m and 120 meters depth. Gravel deposits like this at such depths are recorded rarely in lakes, but are common in the swash zone of shorelines. Ponar sampling also confirmed the gravel was "well rounded", as claimed by Owen et al. (1990), and was essentially devoid of sediment. It seems it was both logical and prudent for Owen et al. (1990) to infer a paleoshore at this locale.

Since then, uncertainty has arisen not only in regards to the age of the stand but initial effort on the quest to find parallel evidence of a paleoshore elsewhere in the lake has provided limited results. From an evolutionary standpoint, Snoeks (2001) questions the recent age of the 120 m low lake stand, and Nicholson (1998) reports another study in the northern basin did not find parallel evidence for such recent changes in lake level (T. Johnson, pers. comm.). More recently, Delvaux (1995) reports the age of the last major low lake stand was 250 to 500 m below present between 42,000 and 25 - 11,000 years ago. After that, Ricketts (1998) reports lake level drops on the order of 100 – 150 m occurred 5 – 10 000 years ago, rather than just a few hundred years.

How can these gravel deposits be explained? If the erosional features are a paleoshore(s), formed between the years 1500 – 1850 as suggested, the mean sedimentation rate of 1.4 mm/yr (Barry et al. 1999) could be expected to result in a minimum of 20 cm of sediment at this site. The gravel deposit at 100 m has a slope equal to the 4 –5 % threshold that Hakanson and Janssen (1983) states is sufficient to cause redistribution, due to the tractive force of gravity. This does not explain, however, the erosional feature noted at 120 m that is 1-2% slope.

Growing evidence suggests that contemporary water movements can extend as deep as the erosional features, suggesting that the patterns of deposition observed may be the result of contemporary water movements. Studies have shown the southern end of the lake, and the south-east arm in particular, are hydraulically active. Density currents and the meta and epilimnia flow in and out of the south east arm in association with oscillation of the thermocline (Eccles 1974, Ribbink et al. 1983) that penetrates to 125 m (Gonfiantini et al. 1979, Duponchelle and Ribbink 2000). Measurement of water current is sparse in Lake Malawi, but in much smaller Lake Biwa an internal wave generated velocities sufficient to resuspend sediment at 52 m (i.e. maximum depth) after a typhoon (Jiao and Kumagai 1995). The erosional features observed logically could result from internal waves breaking on the lakebed. This may explain why areas of gravel (a rare bottom type except near rift scarps) with slopes less 2%, are sediment free. At 120 m a depositional bottom is predicted (equation 25, Rowan et al. 1992), even when provided a conspicuously high maximum fetch of 230 km). Results of this model in Lake Malawi should be considered tentative because the model is derived from temperate lakes, including the Laurentian Great Lakes, but most are smaller than Lake Malawi. Topographic highs apparent in navigation charts north of our data could modify currents entering the southwest arm, suggesting local hydrodynamics may have produced the surficial patterns of deposition observed.

Contemporary water movements and surficial bottom sampling cannot, however, explain the origin of the gravel deposits. While gravel is a rare bottom type at great depth, this study benefits from extensive lake wide habitat observations. It has been shown clearly that gravel is strongly associated with (i.e. adjacent to) rift scarps, such as Domwe

Island. In summary, contemporary water movements may explain the surficial pattern of deep water deposition, and the superimposition of sediment on a large sand/gravel deposit could create the appearance of gravel bars. Alternatively, contemporary water movements may continue to cleanse a paleoshore established by historic low lake stands.

4.3.4 The Tectonic Framework and Regional Mbuna Species Composition

The similarity between the regional distribution of the rocky dwelling mbuna and the tectonic framework of the basin is clear (Figure 4.9). Recently, Snoeks (in press) provided an insightful analysis of the distribution of 282 rock dwelling mbuna species from 136 localities distributed around the lake, using the data of Konings (1996). From this, Snoeks was able to distinguish 21 regions that generally had similar faunal composition; 13 of which were on the mainland coast. As shown in Figure 4.9, the pattern of these regions reflects closely the polarity of the half grabens. Few discontinuities are found on border faults, except in places where depositional relief intersects the coast. Examples of this include the Maniamba trough found on the Metangula half graben, regarded by Snoeks as the Cobwe/South Central Transition. Similarly, depositional relief provided by a river delta 2 km wide near the discontinuity evident between the Livingstone and PaleoEast faunal region appears sufficiently large to provide a barrier to the movement of many species, but the many short gravel deltas found on the Livingstone border fault to the north apparently do not. The similarity of fauna along the Livingstone mountains was also noted by Spreinat (1995). The extent of the PaleoWest faunal region is surprising given that an En Echelon fault (Crossley 1984) of depositional relief 12 km in length divides the Usisya Border Fault. The northern extent of this region, north of Chilumba, is erosional relief eroded from the side of a horst block (Owen and Crossley 1989). This area is included in Snoeks' PaleoWest region despite the fact that nearly 30 km of depositional relief (with negligible rock) is found south of Chilumba. The Makanjilla faunal region corresponds to the submerged side of a single tilt block. Relief on land is limited, but an abrupt and extraordinarily steep shelving rocky littoral with unstable boulders (A. Konings pers. com) reveals the fault along the west edge noted by Crossley (1984). This tilt block, like many of the other tectonic units in the basin, has predominantly fine grained materials in the zone of accommodation between adjacent tectonic units. In this case a 9 km stretch of beach marks part of the transition, and also northern extent of the Makanjilla faunal region. The Southern and Northern faunal regions are found on depositional relief found on shoaling margins and have few rocks, or in the case of the latter, no rocks in the coastal zone. These regions largely can be discounted from the pattern.

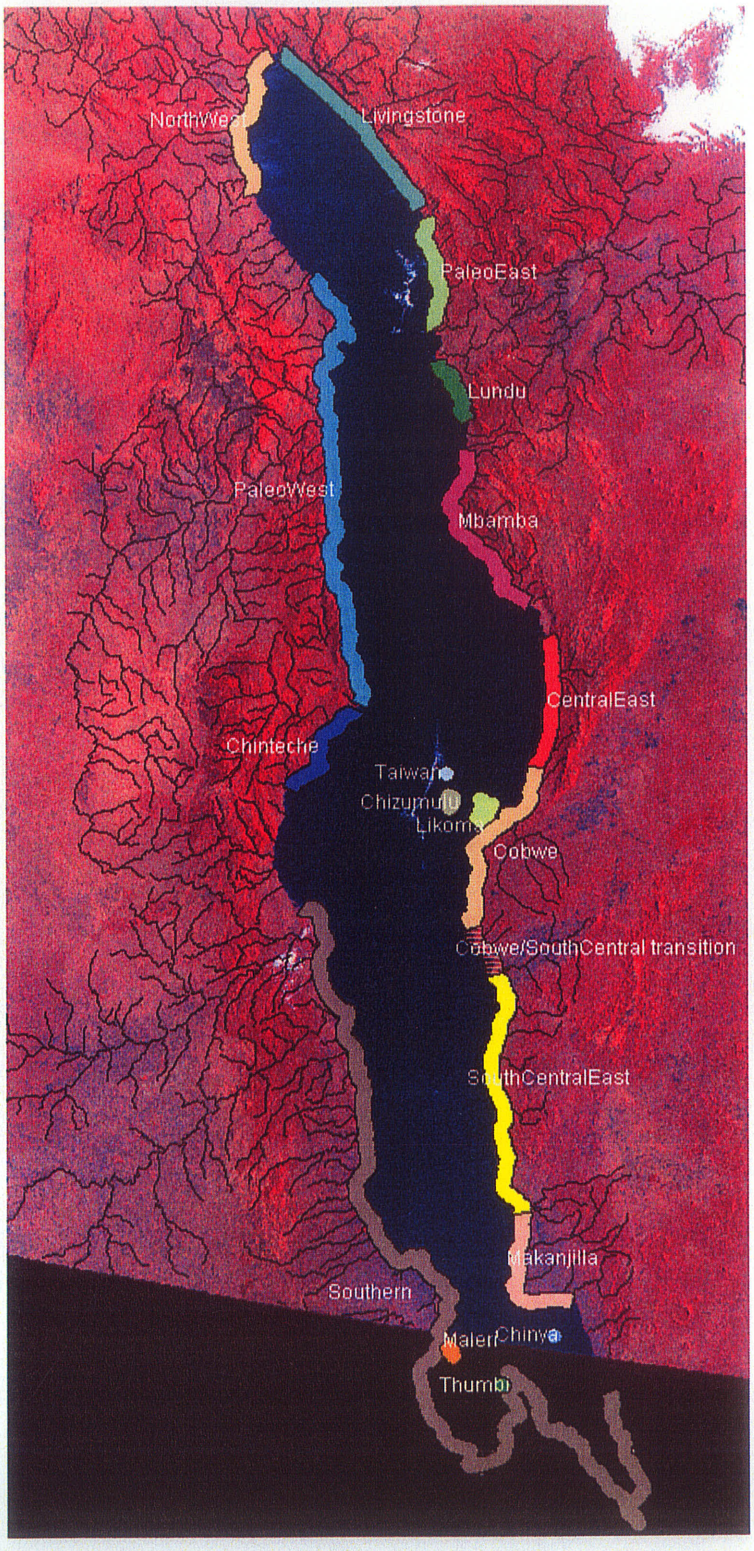

Figure 4.9. Icthyogeographic regions define large areas of the lake with a similar rock dwelling mbuna fauna (from: Snoeks, in press). The faunal regions demonstrate a strong regional signal that reflects closely the tectonic framework of the Malawi Rift (see Figure 4.9).

4.4 Conclusions

The objectives of Chapter 4 were to: 1) Relate the distribution and composition of the coastal zone to the tectonic setting. 2) Assess the scale of coastal habitat discontinuities by comparing the size (i.e. length and depth) of the main coastal types according to landform. 3) Validate the character of a littoral site described in the literature as a low lake stand 120 m below present. 4) Show the influence of the tectonic structure of the Malawi Rift on the regional distribution of species composition.

Objective one was addressed in the section "the tectonic framework, geomorphology, and coastal habitat". The amount of the coastal zone represented by three geomorphologic regions, three classes of slope, and eight classes of coastal type was described as was the correspondence between these variables. The lakeshore plain is the dominant landscape that the coastal zone bisects (85% by length). Sand and Sand/Vegetation coasts dominate this topography (59%). Rock is found only on 25% of the coast, and most of this rock (95%) is found in erosional and rift scarp settings. Correspondence analysis and the empirical data showed clearly that rift scarp settings tend to be rock and high slope (>8%), whereas depositional areas of the lakeshore plains are mainly vegetated and low slope (<4%). Erosional coastlines appear juxtaposed between these two; habitats in this topography have a moderate slope (4 - 8%), a higher number of classes, and most of the mixed classes. Accordingly, the slope of the geomorphologic regions are significantly different and provides corroborative evidence for differences observed. It becomes apparent that habitat heterogeneity is low at the extremes of slope found on rift scarps and depositional areas of the lakeshore plains, and is higher in the moderately sloped erosional topography.

Objective two was addressed in the section "Habitat Discontinuities". The sum of length in each type of coast showed the coastal geomorphology is a strong indicator of the predominant material types and also sets the scale and continuity of coastal habitat. The length of rock, sand, and vegetated coasts each are significantly different when compared by landform, indicating the major and minor constituents of the coast can be inferred by the geomorphologic setting. Pair wise comparisons by class demonstrate in most cases the length of coastal segments are significantly different across landforms, except for rock (deposition vs. erosion) and sand (rift scarp vs. erosion). Again, it appears that the greater number of classes on erosional coasts results in shorter coastal segment lengths. The trend of decreasing length of coastal segments from rift scarp to depositional areas is mimicked also by the depth to the rock/sand boundary, confirming the apparent scale differences in the habitats observed horizontally around the basin ordinate in the same order as water depth increases.

Objective three was addressed in the section "The 120 m low lake stand". A decade after the original field work, this study confirmed the attributes that lead Owen et al. (1990) to claim a low lake stand on the east shore of Domwe Island, using sonar and benthic sampling. The interpretation of historic processes using contemporary substratum patterns, however, is uncertain. On one hand, the surficial substratum contained "well rounded" gravels and showed a banding pattern and slopes typical of many shorelines, suggestive of a paleoshore. On the other hand, this study also showed that gravel deposits are rare but when found are almost always near a rift scarp, such as Domwe Island. It was argued that the patterns observed also could result from a combination of water movements maintaining the erosional features and superimposition of sediment on top of the sand/gravel deposit. In either case, it appears that contemporary water movements are responsible for maintaining the patterns observed, but the origin of the gravel feature remains uncertain.

Objective four was addressed in the section "The tectonic framework and regional mbuna species composition". The strong correspondence between the tectonic framework of the basin and the major coastal habitat type was demonstrated in objective one. Using recently published information (Snoeks, in press) the pattern of regional species composition also appears remarkably similar to the distribution of coastal habitat, implying a strong influence of the tectonic framework of the basin on the regional distribution of species. The largest faunal regions appear to occur along border faults where objective 2 demonstrated that most of the coast is rock, and discontinuities are relatively short. Discontinuities in rock habitat that correspond with Snoeks' ichthyogeographic regions appear to be river deltas, both as a minor habitat (i.e. short discontinuity), and also when deltas or beaches are set within larger depositional zones of the lakeshore plains. In some cases it appears relatively short discontinuities (2 km) provide sufficient barriers to dispersal for many species. In others, such as the extensive PaleoWest, the faunal regions may span discontinuities more than 20 km long. These regions are considered preliminary by Snoeks so further sampling may show substructure within the PaleoWest faunal region, as would be expected according to rock habitat distributions.

4.4.1 Summary

In summary, rift scarp, erosional, and depositional landforms represent a basic topographic sequence that forms three distinct types of coast. These express both a major regional pattern of habitat alternation reflecting strongly the underlying tectonic framework of the basin, and also a gradient of habitat scale. The alternation of rift scarp and lakeshore plains set up by the dip polarity of the half grabens isolates sections of predominantly rock coast on the order of about 100 km. Any rock coast found along the edge of a major border fault is isolated from the next by a shoaling margin with mainly sand or sand/vegetation to the north, south, and also on the opposite coast. Therefore, rocky coasts along border faults are geographically isolated from those of the adjacent half graben(s), and at a regional scale, may be perceived as linear islands. Discontinuities within the regional geomorphology also segment the habitat at local scales. Rock habitats, therefore, appear to be structured hierarchically. The regional isolation of a rock border fault coast appear to mimic the mechanism of macroallopatry offered by isolation of separate basins during low stands (as suggested for Lake Tanganyika). Within a region (i.e. half graben), the conditions may also be favorable also for microallopatric divergence, given the high degree of segmentation of the Lake Malawi coast. Konings (2001) shows many examples of segmented distributions within the faunal regions. This supports the notion of regional metapopulations of mbuna.

This chapter contributes to a growing consensus that low lake stands 120 m below present may not be as recent as reported. Under this scenario, it appears that for the past 5 – 10 000 years since the major last low lake stand allopatric mechanisms have operated mainly as a shore sequential (i.e. horizontal) process, rather than one that has been moderated recently by lake level variation. This chapter has provided a physical framework that demonstrates the horizontal distribution and vertical dimension of the mbuna rock habitat. I have also shown that the general distributions of the mbuna mirror the regional habitat patterns. This result indicates conservation planning for the mbuna should be stratified both regionally (i.e. according to the distribution of the half grabens) and also locally. It is apparent that the design of parks/reserves can use the extent of rock, i.e. in both the horizontal and vertical sense, to delineate park boundaries. The offshore side of a park will be limited to relatively shallow water due to the limited depth that rock is found.

The horizontal distribution of habitats for the lake and the vertical extent of the rocky zone is now documented for the first time. The focus of Chapter 5 is to determine if the sandy regions of the lakeshore plains also have substratum discontinuities that might separate the nearshore and offshore habitats, and potentially influence the species composition. A subsequent chapter investigates the distribution of species composition within the lakeshore plains.

Chapter 5 The Littoral Habitats of the Southern Basin of Lake Malawi

5.1 Introduction

In this chapter, I continue to examine the theme of habitat discontinuities started in Chapter 4, but the focus shifts from the segmentation of the coastal zone in the horizontal sense to explore discontinuities that occur vertically (i.e. as water depth increases). In Chapter 4 the coastal habitat framework was shown for the entire lake, as was the depth to the rock/sand boundary in each of the three landforms. In this chapter, the depth of the rock/sand boundary is documented but emphasis is directed to the unstudied deep water setting within the Lakeshore Plains because it is the main landform surrounding the lake.

As described in Chapter 2, the processes of erosion, transport, and deposition are key in controlling the composition and distribution of substrata in lakes. These forcing functions result in the differences frequently observed between the coarse grained and high energy environments in shallow water, to the fine grained and sedimentary areas found in deep water. Clearly, the interpretation of erosion, transport, and deposition processes is important to understand *why* distributions are as they appear, and mass wasting (i.e. the result of these forces) is not limited to aquatic environments. In Chapter 4 the synthesis of the underlying reasons for the coastal habitat distributions resulted from relating them to the geomorphology of the basin. The rift scarp, erosional, and depositional landform (i.e. shape) classes correspond generally to the erosion, transport, and deposition process variables, respectfully. This enabled cognitive abstraction that simplified the interpretation of how the tectonic form of the basin controls habitat availability. Indeed, as shown in Chapter 4 at the site of a reported low lake stand, an understanding of these forces also helps to interpret the relative roles of variables that create and maintain littoral habitat distributions. The main focus of this chapter, however, is to identify and demarcate the substratum patterns, rather than to explain them in the quantitative context of forcing and response. This approach recognizes the variables that form littoral habitat distributions (e.g. wave energy and slope) are, in principal, reasonably well understood but their spatial consequences (i.e. habitat patterns) are not.

The southern basin of Lake Malawi is adjacent to the Linthipe Watershed, an intensively cultivated basin that is the second largest exporter of sediment to the lake (Mkanda 2002, Kingdon et al. 1999). Because the rate of sediment entering the littoral is higher at sites that are close to sources of sediment than are those that are distant and unaffected, the southern basin presents an unique opportunity to compare and contrast the character of deposition across a series of sites that are perceived to be in a steady state condition (i.e. unaffected by recent perturbation and represents a temporally invariant character on an annual time scale) to another that is close to a source of sediment.

The need for information about littoral substratum composition and pattern is threefold: 1) to determine if habitat discontinuities are present as water depth increases. Such a habitat boundary would enable the inshore and offshore zones to be distinguished and provides a logical basis from which to compare species composition, 2) to examine the substratum pattern at a scale that is sufficient to validate the character and consistency of the pattern unambiguously over small spatial scales (i.e. large areas). Mapping large areas ensures the patterns observed are not unique to the study sites, and 3) to use inter-site comparisons to better understand the difference between sites in a steady state condition to one that is not. The research questions of this chapter are as follows:

1) *How are the physical properties of the substratum related to their acoustic signatures?*
2) *Can the acoustic signatures be used to discriminate and classify the littoral substratum?*
3) *Does the upper depth limit of silt/clay deposition form a boundary (as opposed to an elongated gradient), and is this depth similar across all 5 study sites?*

These questions condense to a need for a remote method for substratum classification and to illustrate substratum patterns by echo sounding large areas in a variety of lakebed topographies, with the important constraint that each study area must extend into the offshore zone. To do this, I present constrained multivariate analyses that are used first to elucidate the relationship between the size constituents and the slope of the lake floor to the acoustic response. Once this relationship has been demonstrated empirically and the use of classes to partition the data has been justified, then the acoustic data are used to classify the littoral substrata.

5.2 Methods

5.2.1 Study Sites and Sonar Techniques

Five littoral areas were investigated in the southern basin of Lake Malawi with a total a mapped area of 140 km^2 (Figure 5.1). All study sites fall within the Lakeshore Plains (see Chapter 4) except for Domwe Island that is rift scarp relief. The remaining six islands (i.e. the 3 islands collectively referred to as the Maleri Islands, Mumbo Island, Domwe Island, and Thumbi Island West) rise as erosional relief from the Lakeshore Plains and are predominantly rocky in shallow water. Senga Bay represents a mainly sandy shore in the depositional area of the Lakeshore Plains.

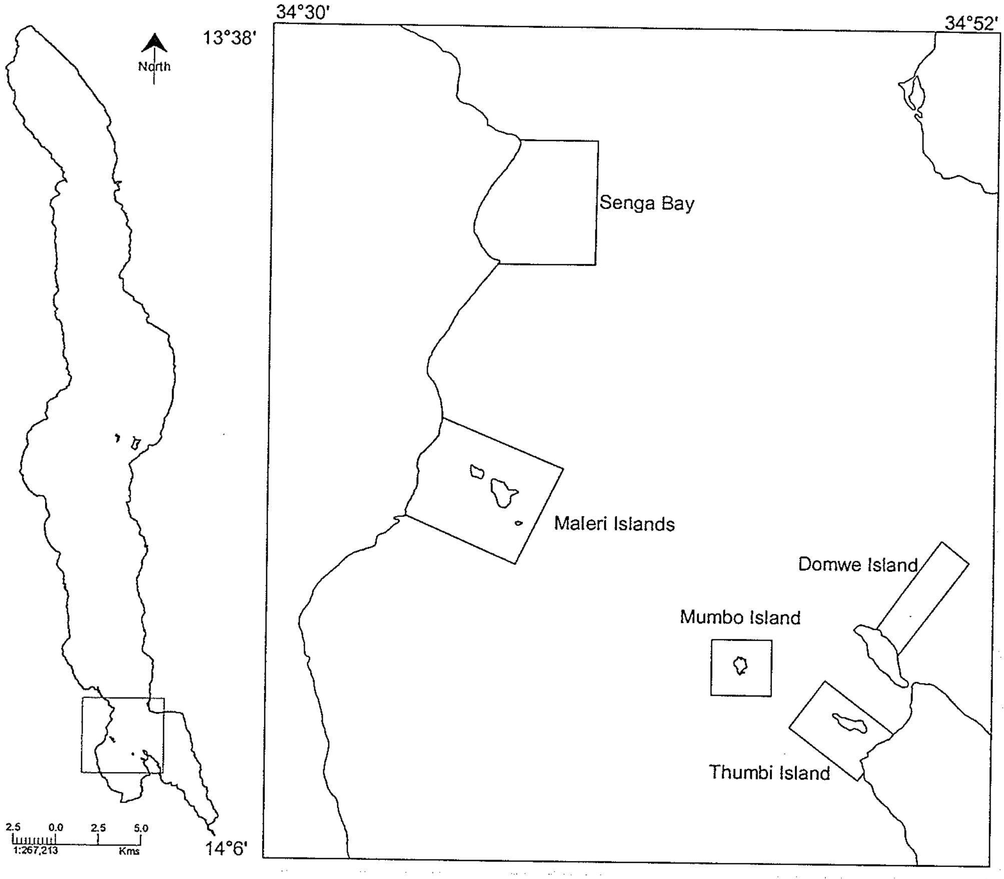

Figure 5.1. Locations of five study areas in the southern basin of Lake Malawi. Areas mapped using sonar are indicated with rectangles and are labelled.

Substratum depth and attribute information was collected using a vertical beam sonar system coupled to a sub-meter Global Positioning System during the months of November - March. Data for the Maleri Islands was collected during November - December before the season of increased sedimentation. The digital echo sounder operated at 120 kHz (12.5 cm wavelength) and used a time-variable gain to automatically adjust signal strength over a wide range in depth. Substratum depth (+/- 0.1 m), hardness, and roughness values were collected using the first echo, at 2 second intervals. Hardness is defined as the peak echo voltage from the substratum in 0.5 decibel units and is expressed as byte data. Roughness is defined as the sum of all echoes from the first lake bottom echo to the second lake bottom echo, and is of the long integer data type. Data collection typically was perpendicular to depth contours. The number of sonar positions for each study area ranges between 7, 000 - 76,000. The average spacing between points on a transect was 5m.

5.2.2 *Sample and Data Processing*

Substratum samples were collected at each site using a Ponar benthic grab representing a range in depth from 2 - 120 m. Samples were processed using either a dry sieving method using a Ro-Tap shaker, or by automated particle size analysis, according to Last (2001). Grain size fractions were aggregated into three classes using phi of 1.0 (2000 um) and 4.0 (63 um) to separate gravel, sand, and silt/clay from which the percent by mass of each class for all samples was calculated. The geometric mean phi (ø) was calculated according to Folk (1980). Each sample was classified as gravel/sand, sand, and silt/clay. The geometric mean phi range for each class was: Sand/gravel (ø = -0.78 – 0.3, n = 9), sand (ø = 0.31 – 3.3, n = 26), and silt/clay (ø = 5.2 – 8.6, n=19).

Validation of boulder/cobble areas first involved SCUBA survey to confirm an entirely rocky substratum of materials ranging in size from 30 - 350 cm in diameter. Boat-based surveys mapped the position of the rock and sand boundary using a 255 colour display of the bottom topography while sounding the bottom material with the ponar as water depth increased. The position of the rock/sand boundary generally was at less than 40 m and was recorded at 30 m intervals along the shore using DGPS. Thirty locations within the rocky zone were added to the total validation sample of 95 localities.

For each site in the southern basin a surface model of elevation, depth (meters), and slope (%) was derived from the sonar data.

5.2.3 Data Analysis

The acoustic data, slope, and benthic sample data was divided into validation and classification treatments for analysis. Redundancy analysis (RDA) was used to illustrate how much variance in the acoustic data could be explained by the substratum composition. In principal, the approach of an RDA is similar to canonical correspondence analysis (CCA), and the method of ordination can be considered an extension of principal components analysis (PCA). As described by Legendre and Legendre (1998), RDA and CCA methods relate two datasets by using one to constrain the ordination of another. Unlike CCA, RDA preserves Euclidean distances and is preferred when the relationships between the two datasets are linear. Like PCA, the canonical ordination vectors of RDA are linear combinations of the response variables but PCA is applied to a single dataset and so is considered unconstrained. RDA was implemented using RdaCca (Legendre and Legendre, 1998). Overall tests of significance between the explanatory and response datasets used 999 permuted iterations of the residuals. The acoustic data were standardized before analysis by adjustment to unit column length as recommended for RDA by Legendre and Legendre (1998). Scalings for distance biplots were used to maintain approximate Euclidean distances and correlations among the explanatory and response variables.

Multiple discriminant analysis (MDA) also is a constrained canonical ordination technique that was used to determine which acoustic variables best accounted for differences between apriori defined substratum classes (rock, sand/gravel, sand, and silt/clay). This classification model was then applied to the sonar data for the five sites to map bottom types and to document the depth of mud deposition. Discriminant analysis results were produced using spherized scores using Syn-tax 2000, (Podani 2001). Cross validation is assessed in all cases using about 50% of the data to predict class membership for the remaining samples for which membership is known. These are referred to as the model and test groups, respectively. The model group was populated using every second observation in the database, ensuring representation from all study areas. Cross validation and classification of the acoustic mapping database was employed using discriminant analysis in SPSS (version 10). Sensitivity analyses were undertaken on the validation data using a series of MDA trials where variables were removed sequentially. The computational method of the MDA technique, also called Linear Discriminant Analysis or Canonical Variate Analysis, was described in Chapter 3.

5.3 Results and Discussion

5.3.1 Physical and Acoustic Properties of the Littoral Substratum

RDA shows the canonical relationship between the benthic validation samples and the corresponding acoustic signatures is highly significant (p = 0.001), providing strong support for development of sonar based classification model. In total, 56% of the variance of the acoustic signatures was accounted for by the sediment composition data. The first two axes explain 87% and 12% of the total variance, and the first axis demonstrates a strong species-environment correlation (i.e. 0.80 and 0.45, respectively).

Two main groups are evident when the acoustic signatures are constrained by the composition of the substratum (Figure 5.2). Axis 1 is dominated by slope and roughness, and separates the heterogeneous acoustic signatures of rock from sand and silt/clay. Acoustic hardness contributes most to axis 2 that separates the high magnitude acoustic signals derived from reflections on rock and gravel from areas of lower acoustic impedance, such as sand and silt/clay. Figure 5.2 also shows that several samples validated to be sand were grouped within the scatter of rock, and so appear to have ordinated spuriously.

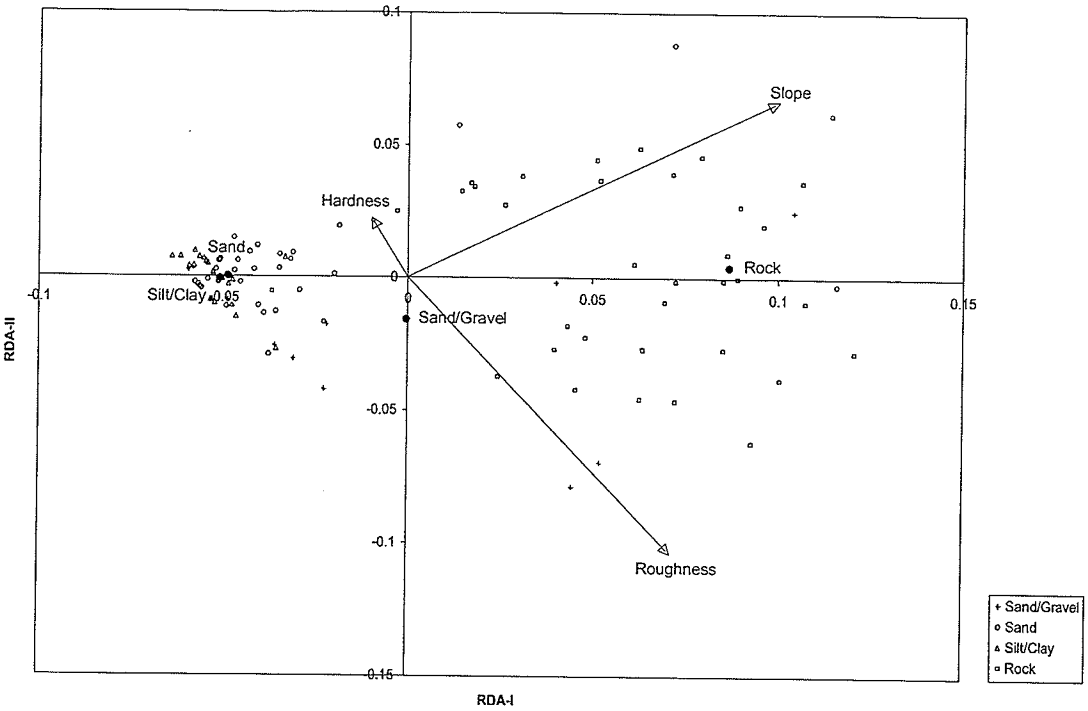

Figure 5.2. Redundancy analysis triplot representing the constrained ordination of the acoustic lakebed signatures (hardness, roughness) and littoral slope (%) by the composition of samples obtained during field survey.

The acoustic and slope validation data are shown in Figure 5.3. Inset A + B show that sand and silt/clay bottom types can be separated at a hardness of about 128, despite being found predominantly in low slope environments with low bottom roughness. The acoustic reflections from rock or sand/gravel are from higher slope environments when compared to sand or silt/clay, but provide heterogeneous reflections that frequently represent the full range of hardness and roughness values shown for the other classes. Therefore, it is apparent that the importance of slope as a discriminating variable appears relatively low for classifications of sand and mud, but is key for classifications that include rock.

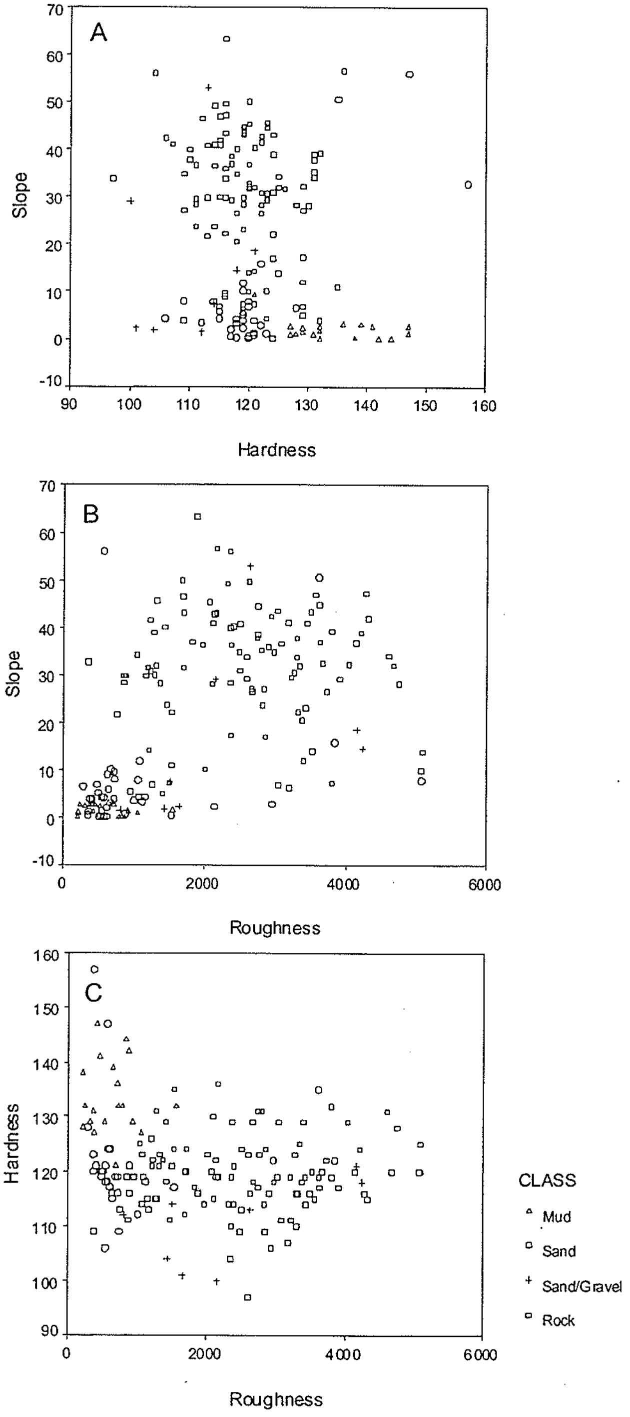

Figure 5.3. Scatterplots of acoustic variables derived from the validation dataset. (A) + (B) compare the hardness and roughness for all samples according to slope, (C) roughness and harness for the validation dataset.

The magnitude of the hardness value is dependent not only the type of substratum but also by the angle of incidence (i.e. littoral slope). Inset A of Figure 5.3 shows three samples of sand, identified first as outliers in the RDA, have hardness values similar to depositional environments, but only on slopes greater than 30%. To investigate the effect of slope on the magnitude of bottom hardness signature, I identified a sonar transect from the area in which the spurious samples were taken, the bottom composition was known, and a large range in slope was evident (Figure 5.4). Along this transect the grain size remained similar (mean ø = 0.50 - 0.57, n = 3). The second half of the transect changed from a level platform at 7 m depth to a littoral shelf that descended to 80 m. The magnitude of the bottom hardness value clearly decreases (i.e. a larger hardness number results and is indicative of a soft bottom) on slopes above 30%, apparently due to oblique reflections of the acoustic signal. Pearson correlations are significant between bottom hardness and slope for sand and rock (Table 5.1). Higher correlations result for sand, perhaps because the planar surface provides a smoother response echo. The correlation for rock could be expected to be lower due to heterogeneous scattering of off single rocks or multi-path scattering from several rocks (Figure 5.3).

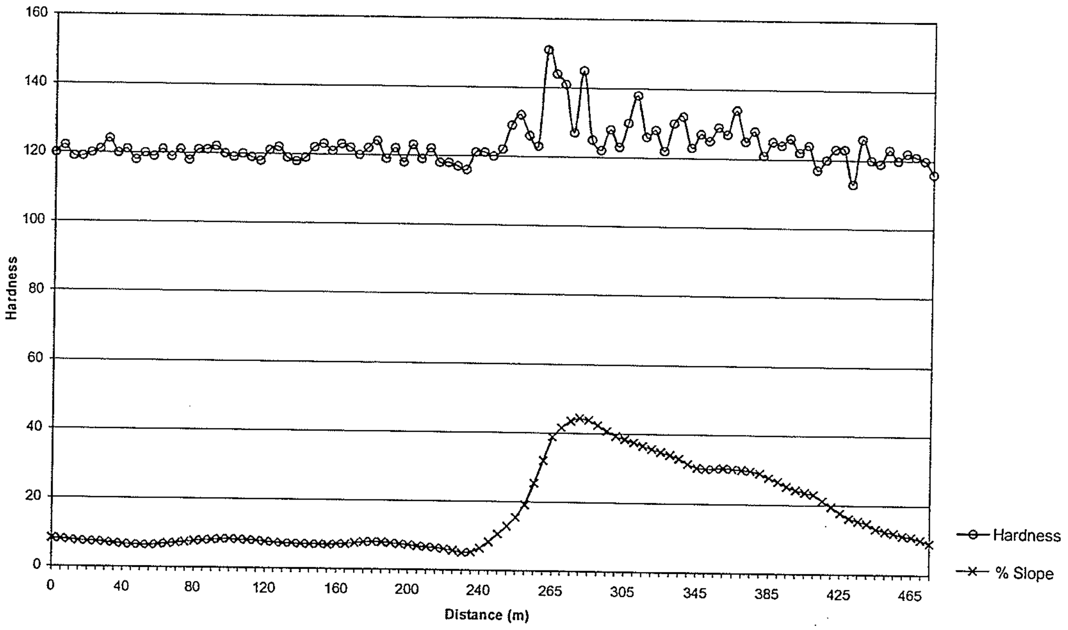

Figure 5.4. The effect of incident angle on bottom hardness. A sand transect is shown where high bottom slope results in oblique reflections away from the sonar receiver, mimicking weak returns from a soft bottom.

Table 5.1. Pearson correlation coefficients derived from the validation dataset of hardness, roughness, and littoral slope. Correlations that are significant at the 0.01 level are shown in bold.

Substratum type	n		Roughness	Slope
Rock	99	Hardness	0.121	**-0.266**
		Roughness		-0.67
Sand/Gravel	8	Hardness	0.62	0.147
		Roughness		0.39
Sand	35	Hardness	0.056	**0.718**
		Roughness		0.169
Silt/Clay	20	Hardness	-0.087	-0.411
		Roughness		-0.064

The causal relationship between slope and hardness can be gleaned from the present data for sand. Unfortunately, this cannot be done for rock because the slope represents the main gradient of the lakebed rather than the slopes provided by an individual rock(s) within the sonar footprint. The present data are not suited to identify a slope threshold that results in a hardness value that is significantly different from that expected from a normal angle of incidence. Such study is complicated by the fact that most abrupt changes in littoral slope also are accompanied by changes in the composition of the substratum, and locations of this sort are challenging places from which to acquire Ponar samples. The diminished hardness reflections evident at high slope are valid signals that can be used in classification. Unfortunately, three points is too small a sample and so was removed from further analysis. No change was noted in bottom roughness at this sandy site.

The amount of gravel in the sand/gravel fraction (>63 um) results in an increase in the hardness (i.e. decreasing values) and an increase in the roughness value (Figure 5.5). The hardness regression shows a trend of increasing hardness as the proportion of gravel in the sample increases ($r^2 = 0.12$), but the slope of the line is not significantly different from zero ($F = 3.76$, $p=0.63$). In contrast, the slope of the roughness regression is significant ($F= 51.1$, $p=0.000$) indicating that discrimination and classification of sand/gravel (in addition to rock, sand, and silt/clay) samples is justified, and that the roughness acoustic attribute is the stronger discriminator for the sand/gravel fraction of the samples.

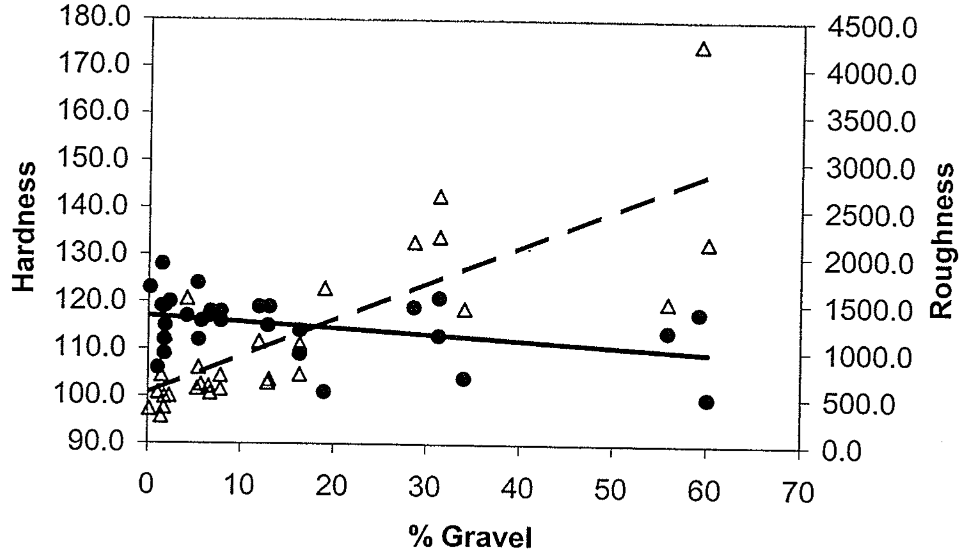

Figure 5.5. The response of bottom hardness (solid circles) and roughness (triangles) attributes as the percent of gravel by mass increases for the sand/gravel fraction (>63 um).

5.3.2 *Discrimination and Classification*

The MDA results replicate closely the earlier findings of the RDA analysis (Figure 5.6), thereby lending strong support both for the use of the selected acoustic variables as descriptors of bottom type, and the choice of the a priori defined classes used in the MDA. The MDA analysis shows a greater separation of the sand and silt/clay groups while also expressing larger point dispersion than was evident in the RDA. This appears to result from the maximal separation of the apriori defined groups according to the MDA technique. The relatively wide scatter of the points in the MDA also suggests the acoustic data are more variable than are the substratum composition data used in the RDA.

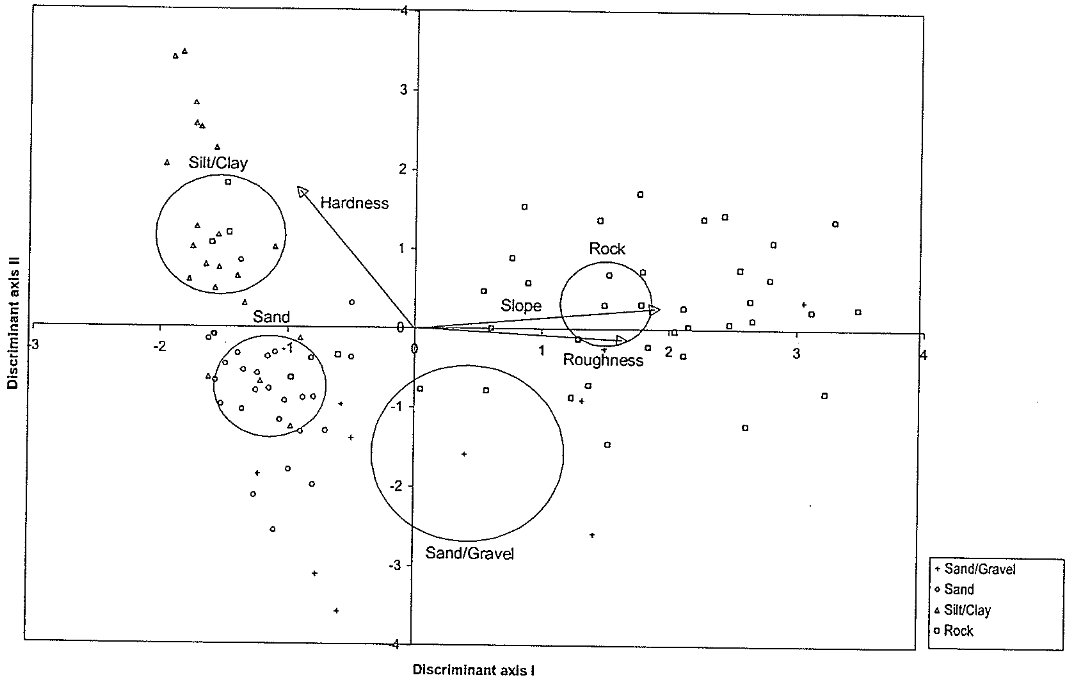

Figure 5.6. Multiple discriminant analysis of acoustic signatures from rock, sand/gravel, sand, and silt/clay substratum. The centroids for each class are bounded by a 95% confidence circle.

The results of the MDA sensitivity analysis are shown in Table 5.2 where the effect of removing slope and/or the rock class on the acoustic variables is compared. The absolute magnitude of the standardized discriminant function coefficients assess the relative importance of the original descriptors to each axis. Like the results of the RDA, the slope and roughness contribute most to the first axis of the 4 x 3 trial (all classes, all variables), and hardness contributes the most to axis 2. As either the rock class or slope is dropped from the model, the variance explained by the first axis increases and a pattern in the standardized canonical coefficients emerges. In the trials where hardness, roughness, and slope are tested, slope and roughness respond similarly in terms of weight to each axis, and inversely with hardness; a response expected from correlated variables. For the comparisons using only hardness and roughness the weights of both are similar apparently because they are inversely related and describe a single trend.

Table 5.2. Multiple discriminant analysis trials demonstrating the effect of varying the number of variables and/or classes. Class key: R = rock, S/G = sand/gravel, S = sand, S/C = silt/clay.

Trial	R, S/G, S, S/C		R, S/G, S, S/C		S/G, S, S/C		S/G, S, S/C	
Discriminant Axis	1	2	1	2	1	2	1	2
Hardness	-0.448	0.866	-0.772	0.636	0.8	0.592	0.799	0.601
Roughness	0.839	-0.071	0.847	0.532	-0.809	0.587	0.814	0.581
Slope	0.957	0.131	-	-	-0.602	0.11	-	-
Canonical coefficient	0.809	0.659	0.749	0.56	0.832	0.568	0.83	0.567
% variance	68.3	27.7	73.6	26.3	82.5	17.4	82.4	17.5

The cross classification results of the sensitivity analysis are shown in Table 5.3. Overall cross validation results for the Test group was similar to the Model group indicating that sample sizes for the model groups were sufficiently large to capture the full range of the multivariate data tested. Misclassification is most notable between rock and sand. Rock only was misclassified as sand, and sand only was misclassified as rock. The effect of removing slope from the discriminant model decreased class agreement for rock by an increase in the proportion of samples misclassified as sand. Although gravel might be the intuitive choice for misclassification in this case, it appears that the similarity between rock and sand arises due to the variability of acoustic signals from rock that sometimes mimic the signal from low slope and softer bottom conditions due to oblique reflections. In contrast, sand/gravel deposits can be found on low slopes and in this study this bottom type provided the highest magnitude hardness signals observed.

The sand/gravel samples demonstrated poor agreement (25%) in all trials except for those that excluded rock where agreement was complete. This suggests the sand/gravel sample size was too small, but only when the highly variable acoustic response of rock was included. In all trials, silt/clay was only misclassified as sand. Interestingly, classification of silt/clay was highest (80%) in the trial that excluded slope. Further, the S/G, S, S/C model (also lacking the slope variable), showed an increase of 10% to a total of 70% from the previous trial. As noted for Figure 5.3 and reaffirmed here, slope offers little in the discrimination of sand and silt/clay environments.

Table 5.3. Classification agreement derived using multiple discriminant analysis (MDA) of acoustic variables, slope, and four apriori defined substratum classes. The model group (n = 49) was used to develop the discriminant model and was applied to the test group for cross-validation. MDA variables: H = hardness, RGH = roughness, S = slope. Class key: R = rock, S/G = sand/gravel, S = sand, S/C = silt/clay.

MDA Acoustic Variables	Classes Included	Model Agreement (%)	Test Agreement (%)	Test				Test n
				Rock	Sand/Gravel	Sand	Silt/clay	
H, RGH, S	R, S/G, S, S/C	83.7	82.6	88.9	25	100	70	46
H, RGH	R, S/G, S, S/C	77.6	73.9	66.7	25	92.9	80	46
H, RGH, S	S/G, S, S/C	87.1	82.1	-	100	92.9	60	28
H, RGH	S/G, S, S/C	87.1	85.7	-	100	92.9	70	28

5.3.3 *The Depositional Boundary*

The upper depth limit to the distribution of offshore mud for each of the study areas is listed in Table 5.4. Deposition in three of the 5 sites can be characterized as a single boundary that is not conformal with the bathymetry, and is continuous with the offshore zone. The Deposition boundary at these sites ranges from 68 - 130 m, although most of the boundary at Thumbi Island is at 82 m (Figure 5.7). At Domwe Island several bands of deposition were noted, as discussed in Chapter 4. Deposition at Mumbo Island is nearly conformable with the bathymetry and found at the depth where the steep littoral meets the lake floor. Each of the previous four sites is distant from any source of sediment and is considered to represent a steady state condition. This is not the case at the Maleri Islands (Figure 5.7) where the depth of persistent deposition occurred in shallower water, up to 28 m, and was heterogeneous.

Table 5.4. Depth of deposition and character of the boundaries at sites studied using sonar. Single boundaries are interpreted as continuous with the offshore zone.

	Range in Depth of deposition	Character of boundary
Thumbi Island West	68 - 82	single
Mumbo Island	100 -102	single
Senga Bay	80 - 130	singe
Domwe Island	82 - 120	multiple
Maleri Islands	28 - 64	heterogenous

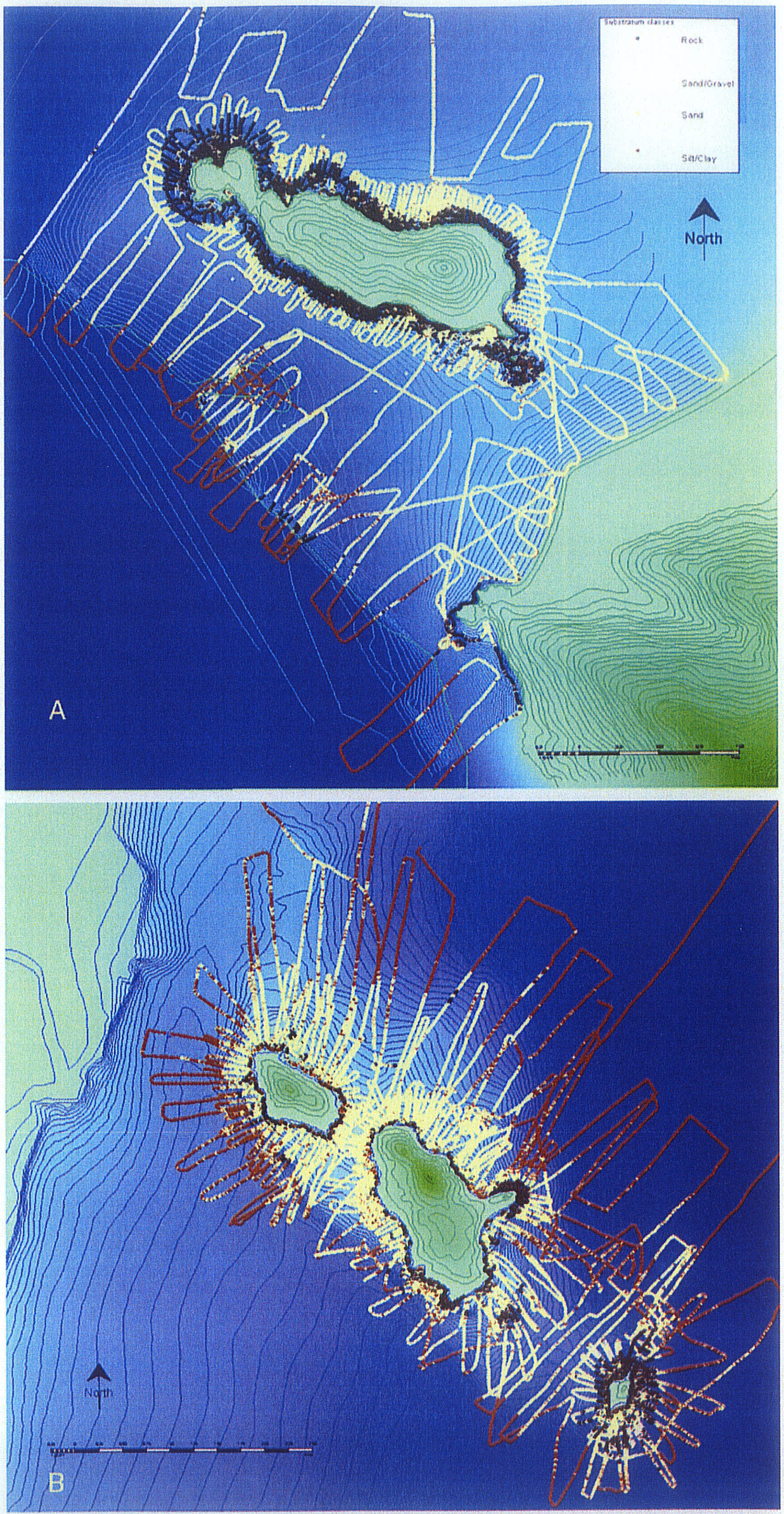

Figure 5.7. Classified sonar tracks for rock, sand/gravel, sand, and silt/clay for: A) Thumbi Island West and B) the Maleri Islands showing the Linthipe River and delta to the west of the islands.

Grab sampling during the rainy season at 28 - 33 m confirmed superimposition of sediment on top of gravel deposits; a condition not sampled anywhere else in the 140 km^2 area mapped in this study. These samples were layered in appearance with darker sediments adjacent to the gravel, and red mud at the top of the sample. The comparison of the upper depth distribution among sites and the layered character of benthic samples provide preliminary evidence for littoral constriction (loss of littoral area due to superimposition of sediments) at the Maleri Islands.

Uncertainty in the interpretation of the sonar data at the Maleri Islands is greater than at the other sites due to the design of the classification model. The model was built from environments in steady state and was applied to one that is not. Implicit in the assumption of the model development was that the classification of mud was independent of sites. It is apparent that for sites in steady state the mud boundary is abrupt; the change from homogenous sand to homogenous mud occurs over very short distances (50 - 75 m). Accordingly, within this short transition mud overlies or is mixed in with the sand. Such transitions were difficult to find, and even more difficult to sample due to great depth and limited size. It is precisely this condition that dominates the shallow zone at the Maleri Islands. While grab sampling validated the general pattern of persistent deposition at the Maleri Islands, and sampling of a sand/mud transition at 68 m at Thumbi Island confirmed a silt/clay prediction (suggesting a predictive bias for silt/clay rather than sand), the ability to discriminate a fine layer of silt/clay (probably 10 - 15 cm) is unknown. As a result, the exact position of the upper edge of the mud boundary remains uncertain. This margin of error is however, small relative to the difference in depositional boundary depths observed between sites in and out of a steady state condition.

5.4 Conclusions

The objectives of chapter 5 were to: 1) relate the physical and slope properties of the substratum their acoustic signature, 2) Assess the applicability of acoustic signatures of the substratum to discriminate and classify the littoral substratum, 3) To determine if the depth of mud deposition forms a boundary (as opposed to an elongated gradient) and compare the depth observed at all 5 study sites. This includes one site that is adjacent to a river known to be the second largest exporter of sediments to the lake.

Objective one was addressed in the section "Physical and acoustic properties of the littoral substratum". The strength of the relationship between the acoustic variables (hardness, roughness), slope, and the constraining grain size variables (%sand, %sand/gravel, %silt/clay) was highly significant. RDA axis 1 was attributed mostly to slope and roughness and captured the trend of smooth and low slope silt/clay and sand environments to the high slope and variable roughness represented by a rock littoral. Axis 2 distinguished mainly a change in hardness that represents a wide range in response for rock, and a relatively small range for sand and silt/clay.

The hardness, roughness, and slope data were compared for rock, sand/gravel, and silt clay classes from the validation samples. Sand and silt/clay classes can be separated visually using only bottom hardness. The acoustic reflections from rock or sand/gravel, that are found mainly on moderate and high slopes provide heterogeneous reflections that frequently represent the full range of hardness and roughness values shown for the other classes. It became clear from the validation data that slope would play a limited role in separating sand and silt/clay, but would be essential when the classification included rock and sand/gravel.

The effect of the angle of incidence on the magnitude of the returned echo was demonstrated over sand and showed high slopes mimic the signature expected at normal incidence from a silt/clay environment. Correlations between hardness and slope were significant for rock and sand and suggest that all classes found at high slope (> 25%) will likely carry this artifact due to oblique scattering. This means validation surveys must stratify sampling across bottom types and in areas of high slope.

The empirical data to this point had shown that discrimination of silt/clay, sand, and rock was likely but the validity of inclusion of the sand/gravel class, in acoustic terms, was in question. Simple linear regression demonstrated that the % gravel in the fine fraction of the samples (<63um) correlated significantly with roughness, and also showed a trend with hardness, but was not significant. Therefore, empirical evidence supports inclusion of rock, sand/gravel, sand, and silt/clay substratum classes to an apriori classification model.

Objective two was addressed in the section, "Discrimination and classification". Four sensitivity trials were employed to assess changes in the relative importance of the variables in discrimination, and the corresponding changes in the classification. Strong parallels were evident between the results of the RDA and MDA and reinforce support for the use of the acoustic variables, and the four apriori defined classes. The removal of a substratum class or slope from the model demonstrated that the highly variable acoustic response from rock was the main source of error in cross-classification. Leaving slope out of the model resulted in a decrease in classification agreement for rock. The increase in the error for classification of sand resulted due to the highly variable acoustic signatures from rock that, when constrained to hardness and roughness (i.e. slope is excluded), is most like sand. Removing slope or rock from the model had little effect on the classification agreement of silt/clay.

Objective three was addressed in the section "The depositional boundary". The upper depth limit of the offshore zone of deposition was frequently abrupt, confirming a boundary condition. This boundary was interpreted from the classified maps to show that littoral systems in steady state have a depositional boundary that is deep relative to those observed in a littoral that receives ephemeral but high inputs of sediment in a deltaic environment. Sonar studies validated by ponar samples confirm sediment boundaries were observed usually at 80 - 82 m, but as deep as 130 m. Slope effects on the depth of observed deposition were attributed to just two sites (not including the 120 m site described in Chapter 4). The depositional boundary on the site influenced by fluvial sediment was estimated as shallow as 28 m and validated at 33 m. The acoustic model cannot account for a layered or mixed substratum suggesting the specific position of the boundary is known less precisely at the sedimented site, and is probably overestimates the depth of mud deposition. However, the uncertainty in the position of the sediment boundary on the deltaic site is small compared to the positions of depositional boundaries found mainly in deep water. This lends support for the notion that sedimentation can result in littoral compression; a bottom-up process of littoral habitat loss.

5.3.4 Summary

In summary, the physical and acoustic properties of the three main littoral environments in lakes are very different. This work demonstrates that just three variables can be used to discriminate and classify these habitats under most topographies. The relative contribution of the acoustic parameters in the discrimination of these classes is a novel result of this work despite the fact this technology has been available for a decade: validation is still rare. As a result, the demonstration of the effect of angle of incidence has on habitat classification is also new. This study also marks the first time the pattern of the littoral habitats in Lake Malawi have been mapped, and the presence of habitat discontinuities in deep water have been discovered. This lends credibility to further explore the hypothesis that habitat boundaries found also in deep water can be used as an ecologically meaningful template to design conservation and management zones.

Chapters 4 and 5 demonstrate that habitat discontinuities segment the coast in the horizontal sense, and the littoral in the vertical. Thus, the main habitat framework in the lake has been derived and could form a 2 dimensional spatial template to serve as a basis for zoning the lake in regards to conservation planning and fisheries management. It has been shown that habitat distributions at the regional (i.e. half graben) scale influence the distribution of the rock dwelling mbuna species ranges, and that these rock habitat distributions extend only to about 40 m depth. The subsequent chapters now shift focus from the physical (spatial) to the biological (spatial and temporal) to assess in part if the habitat boundaries at local scales influence species composition, and to investigate differences in assemblage structure and richness.

Chapter 6 The Effect of Space, Time, and Environment on Haplochromine Cichlid Composition in Rock, Sand, and Mud Habitats of Lake Malawi

6.1 Introduction

This chapter investigates the notion that biodiversity conservation in a species rich system could be improved if an understanding of species ranges was included in the design of parks or fisheries management zones. In this manner, the natural discontinuities in species ranges could be realized by changes in species composition, and honored by scientific and management initiatives. Implicit in this approach is that different assemblages can be segregated, i.e. either spatially and/or temporally. The importance of such an approach recognizes that different assemblages may have different range requirements, and the riparian nations may perceive different end uses for each assemblage. Therefore, this approach can support the design of conservation plan that caters to the evolutionary needs of the assemblages to better harmonize biological history with the need to zone resource use around the lake.

In Chapter 4, it was shown with compelling evidence that justification exists for stratifying the allocation of parks for the rock dwelling mbuna based on the half graben structure of the basin. These rocky coasts are temporally invariant in their position and composition and so provide a reliable proxy for mbuna distribution in space and time. In Chapter 5 it was also shown that the mud boundary is also a major habitat boundary in deep water. The mud boundary provides a way to zone the inshore waters from the offshore waters that is both convenient and logical; it is relatively easy to find, and is by definition, a way to demarcate the boundary between the littoral and profundal (Busch and Sly 1992). Does the mud boundary influence the composition of the fishes inhabiting the lakeshore plains?

Spatial and temporal study of the haplochromines is a key perspective from which conservation strategies can be developed, and is particularly important in species rich systems. The study of space (i.e. distance) represents an important evolutionary gradient that can illuminate the relative importance of changes in species composition as a function of distance. This could provide valuable information about how large any parks or management zones should be. Temporal study is essential to more fully appreciate the true species composition due to the relationship between sampling effort and species richness. Temporal datasets also can assess the relative effect(s) of persistent or ephemeral changes in the environment on species composition. In other words, repeat sampling of a series of sites that cross marked environmental gradients not only may show the response of the species composition to a temporally persistent gradient but could illustrate if the ephemeral influences, such as water temperature or total suspended solids (TSS) also have an effect on the species composition.

In this chapter, I provide a comparative synthesis of temporal datasets collected from rock, shallow sand shores, and offshore samples in the southern basin of Lake Malawi. This region of the lake is important to study because it is a depositional area of the Lakeshore Plains and is representative of the dominant type of coast. The area has numerous rock islands, a large and relatively shallow offshore zone and extensive sandy littoral areas. It also is adjacent to the Linthipe Watershed that is the second largest exporter of sediment to the lake during the 5 month long rainy season.

The objective of this chapter is to examine how space, time, and environment (depth, substratum, temperature, total suspended solids), interact to influence the composition of haplochromine cichlids. In so doing, I provide basic insight into the evolutionary and environmental gradients influencing the distribution and composition of the haplochromine cichlids. The research questions of this chapter inter-relate closely and are:

1) *Do habitat discontinuities at local scales influence species composition, and is there evidence to suggest that ephemeral changes in the environment cause seasonal shifts in the composition?*
2) *What are the relative roles of evolutionary and environmental variables that account for variation in the species data?*

To do this, I study three large temporal datasets at 23 sites spanning a large range in depth (0 – 125 m) using repeat sampling of sites for up to a one year period, using multivariate analyses that combines the suite of variables for rock, sand, and mud samples. Unlike previous chapters where each research question was addressed in a specific section, this chapter examines the questions according to each sampling method.

6.2 Methods

6.2.1 Study areas

The study sites represent rock, sand, and mud habitats ranging in depth from 0 - 125 m in the southern basin of Lake Malawi (Figure 6.1). These site were sampled using three methods: SCUBA, seine net, and bottom trawling from June 1998 to May 1999. The mature male mbuna of the rock habitats were studied using SCUBA at one-month intervals from December – May at two sites each on Thumbi Island West (Site 8 and Site 13) and Nakatenga Island (Exposed and Sheltered). In total, sixty SCUBA transects of dimension 2 x 25 m at 2, 6, and 10 m depth enumerated 46 species. The sandy shore haplochromines were sampled biweekly from September to May at five sites (i.e. Nkama, Nsala, Kambiri, Senga Bay, and Lifuwu) resulting in a minimum of 150 species from 70 samples, using a 100 m beach seine pulled towards shore, from 0 – 5 m depth. The offshore haplochromines were sampled monthly from June to May over sand and mud substrata using a bottom trawl with a 4.5 m opening at depths of 10, 30, 50, 75, 100, and 125 m, except during September. The trawl surveys collected a minimum of 127 species. The average length of each trawl was 1.54 km.

This chapter and subsequent chapters refers to the samples by their method of collection, using the following terminology: 1) rock shore (SCUBA), 2) sandy shore (seine 0 - 5m), 3) offshore samples refers to the trawl samples after Turner (1996) given that most samples at 10 m in the sandy areas of the lake are quite distant from the shore. The range in distance between the sampling sites for the rock shore, sandy shore, and offshore samples was 23, 28, and 37 km, respectively.

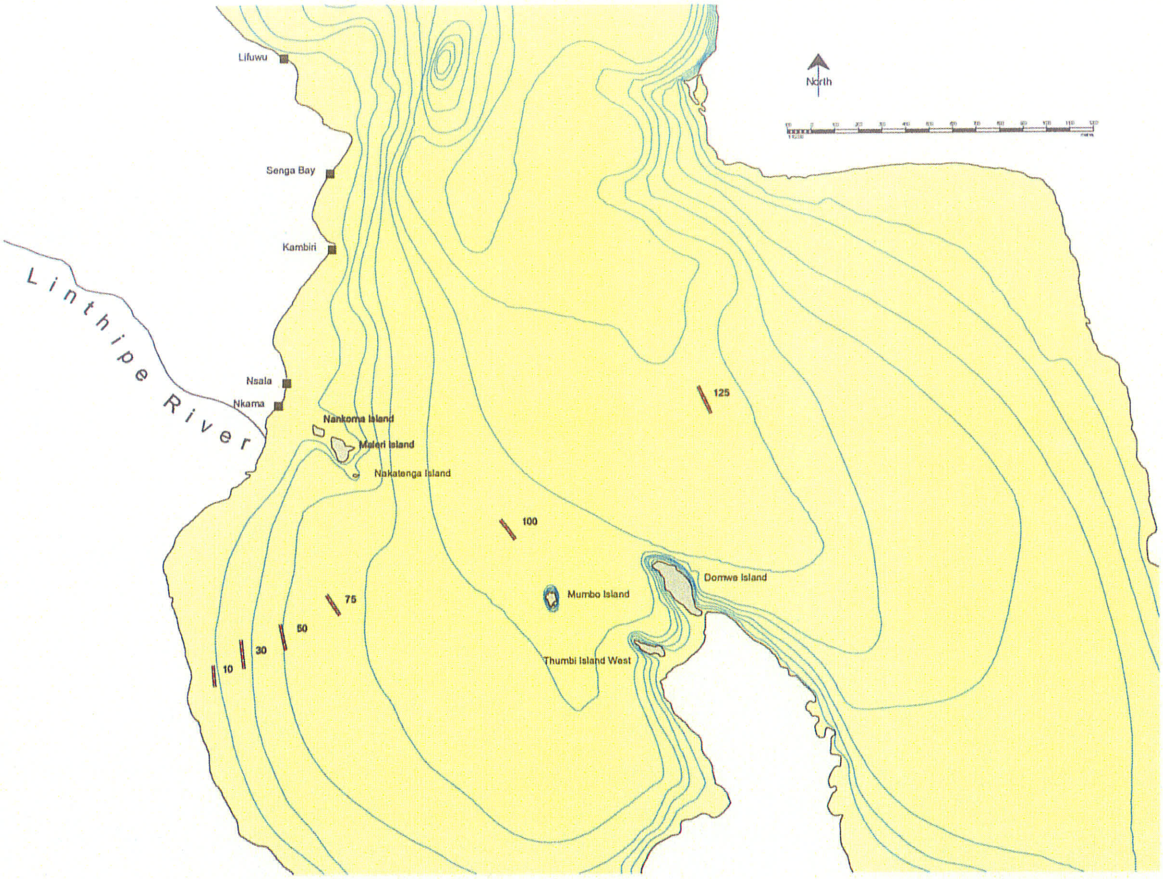

Figure 6.1. Location of the Haplochromine study sites. The rock dwelling mbuna SCUBA surveys at Thumbi Island West and Nakatenga Islands, the sandy shore beach seine sites (black squares), and the offshore bottom trawling sites (dashed lines) in the southern basin. Contour interval is 20 m.

6.2.2 Analysis Methods

Canonical Correspondence Analysis (CCA) (Ter Braak 1986) is a direct gradient technique that relates species relative abundances to environmental variables simultaneously (Gauche 1982). CCA is an extension of the parent method, Correspondence Analysis (CA). CA is an indirect gradient method meaning the ordination of species scores results from the species data only, and the ordination of site scores is done post-hoc. As noted by Ter Braak (1986), similar solutions between these two methods infer the environmental variables included in the CCA analysis account for the main variation in the species data. Unlike some multivariate methods, CCA does not require the assumption of a linear relationship between species abundances and the environment, and the number of species can exceed the number of sites (Ter Braak 1986) as is expected in species rich samples.

CCA is used to investigate the effects of Space, Time, and habitat variables on composition of the assemblages. The analytical framework for analysis of the temporal samples rests on three main approaches for each dataset: 1) I compare graphically the results of indirect (CA) and direct (CCA) gradient analysis to corroborate the relevance of the variables, 2) the analytical strengths of CCA are used to understand how the environmental variables (i.e. Space, Time, Depth, Substratum, Temperature, Total Suspended Solids (TSS) relate and ordinate, and 3) a hierarchical clustering technique is applied to the species data to further support the multivariate results. The hierarchical method is useful for these data because pattern in the cluster dendrogram is more evident than in the biplots where sites and species are tightly grouped.

The haplochromine relative abundance data were square root transformed prior to analysis. The CA analyses were down weighted according to McCune and Mefford (1999). For the CCA analyses, the axis scores were centered and standardized to unit variance, axes were scaled to optimize representation of species, and the sample scores were derived from species (i.e. the WA scores of Palmer 1993). The "inter-set" (Ter Braak 1986) correlations between environmental variables and the WA scores are provided, after the recommendation of McCune and Mefford (1999). Hierarchical clusters were produced using Ward's linkage and the Relative Euclidian (i.e. chord) distance methods. All multivariate analyses used the PC-ORD software program, version 4.27 (McCune and Mefford, 1999).

The haplochromine data have a wide range in assemblage evenness and abundance. To graphically present the combined effects of relative frequency and relative abundance in the multivariate plots the species were classified according to total abundance: 1) rare (≤10), moderate (10 – 50) and abundant (≥50).

6.2.3 Environmental Variables

The variables included in the CCA analyses were: Space (UTM easting for the SCUBA and trawl survey sites, or UTM northing for the seine sampling sites), Time (Julian date), Depth (m), TSS (mg/l), and the mean water temperature within 20 m of the bottom. The rock shore analyses were constrained to Space, Depth, and Time. The sandy shore samples were limited to Space, Time, and TSS. Depth and Temperature were excluded given a small range in depth (0-5 m) was sampled, and partitioning of the seine hauls by depth was not possible. The southern most sandy shore site at Nkama is 1.3 km from the Linthipe River; a major source of TSS to the study region. The sediment plumes entering the southern basin are seasonal and in step with regional precipitation that begins in December but peaks in January/February. The plume frequently deflects to the northeast as the sediment becomes entrained in lake currents. All rocky shore samples were within the rocky zone (similar substrata), within 10 m water depth (near surface water temperature), and in the case of the study sites at Thumbi Island West were distant from rivers and were unaffected by TSS. The offshore data represent a relatively large range in Depth and Temperature, with marked differences in the composition of the

Substratum, and potentially a large range in TSS because the trawl sites range from near the coast to 37 km away in the offshore zone. The offshore variables included were: Space, Time, Depth, Temperature, and the composition of the Substratum (% silt/clay), and TSS. The water temperature and TSS values were estimated from CTD profile data collected at each survey of each trawl site (see Duponchelle and Ribbink, 2000). TSS was estimated using the calibrations and equations of McCullough (2000) and was transformed using the square root. No CTD data were available for February 1999. These values were replaced with the average of the January and March samples.

6.3 Results

6.3.1 Rock Dwelling Mbuna

The ordination by CA for the rocky dwelling mbuna is remarkably similar to the CCA results shown in Figure 6.2. This similarity in solution implies that the environmental variables used in the CCA account for the main variation in the species data (Ter Braak 1986, Legendre and Legendre 2003). This is confirmed in Table 6.1 where 46% of the variance in the species data is explained; nearly all of this is accounted for in the first two axes. The large eigenvalues show that the extracted environmental gradients are long (cf. Gauch and Stone 1979) for the first two axes.

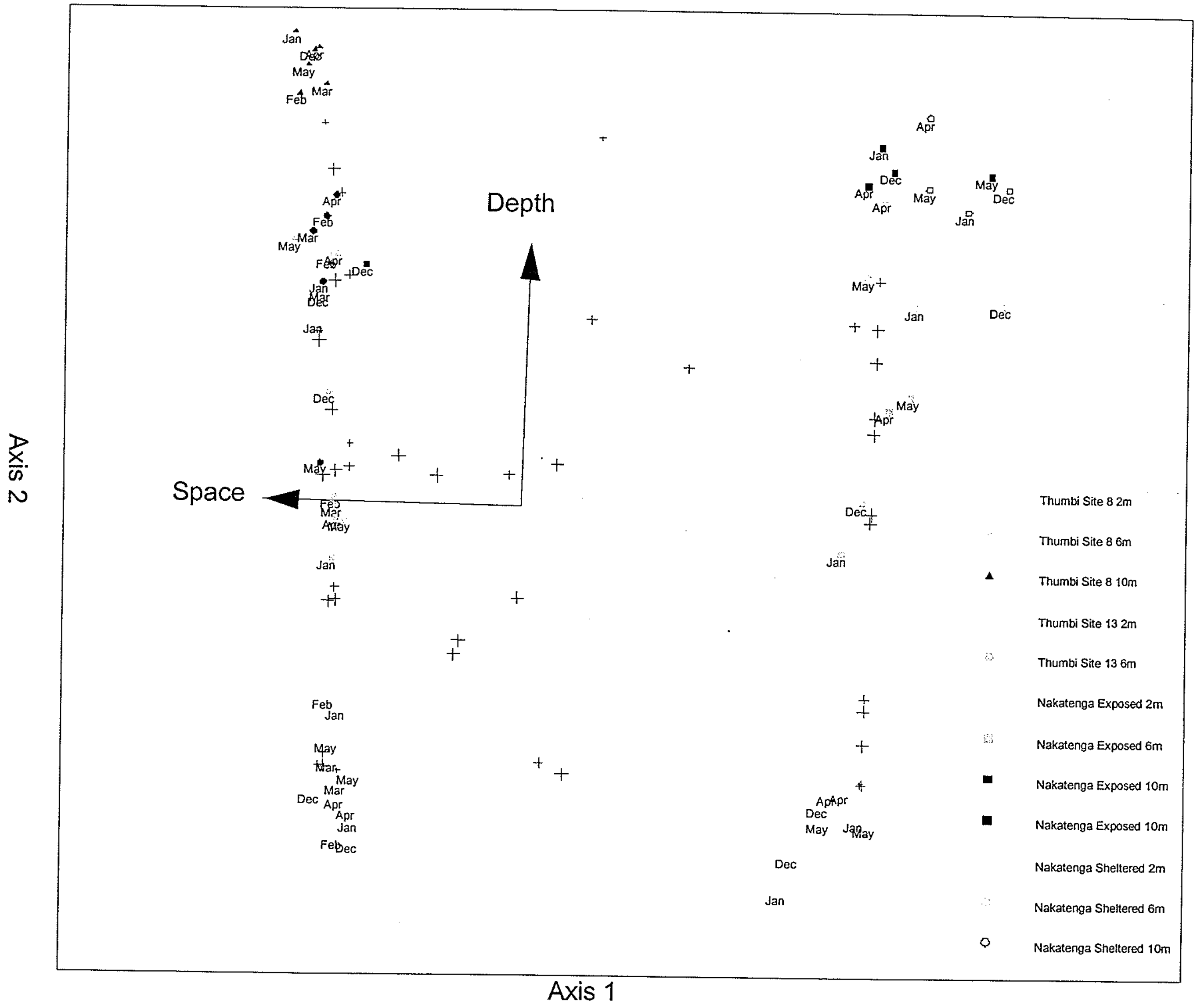

Figure 6.2. The species composition of rocky shore mbuna species (crosses) and sites (other symbols) using CCA for 2 sites each at Thumbi Island West (left group) and Nakatenga Island (right group). Larger cross size symbolizes increased abundance. Crosses at center of the plot are species common to the two islands.

Table 6.1. Eigenvalues, species-environment correlations, and % variance accounted for by each axis for 3 CCA axes derived from rocky shore mbuna surveys conducted at one month intervals from December 98 – May 99. λ = eigenvalue, r = species environment correlation, % = percent variance explained in the species data.

	Axis 1	Axis 2	Axis 3
λ	0.731	0.343	0.01
r	0.992	0.933	0.511
%	31.2	14.6	0.4

The interpretation of the axes is unambiguous because the canonical coefficients of the variables are orthogonal (i.e. uncorrelated) meaning an axis can be interpreted as a single variable (Table 6.2). The signs and magnitudes of the correlations and of the canonical coefficients infer the relative importance of each environmental variable for predicting the assemblage composition. Axis 1 represents Space, clearly separates the two island faunas, and accounts for 65% of the explained variance. Nine species are common between the fauna sampled and are located centrally in Figure 6.2. Axis 2 shows that the mbuna species composition is structured strongly by depth. The CCA biplot appears as two columns of species and site scores given both sites on each island are near when compared to the distance between islands (i.e. axis 1) and the extracted depth gradient is strong and uncorrelated with axis 1. The Time variable explains little variance as made clear by the grouping of samples by depth (Figure 6.2). This indicates the species composition at each depth is stable over time.

Table 6.2. Canonical coefficients and interset correlation coefficients from a CCA constrained to Time, Space, and Depth for the rocky shore mbuna data.

	Canonical coefficients			Correlation coefficients		
Axis	1	2	3	1	2	3
Time	0.001	0.020	-1.000	-0.075	0.017	0.510
Space	-1.000	0.026	0.076	-0.992	0.023	0.000
Depth	0.026	1.000	0.017	0.028	0.932	-0.010

The hierarchical clustering dendrogram of the species abundance data also shows a large difference in the species composition between islands, and provides support for the multivariate analysis (Figure 6.3). Separation between island fauna is clear at the top (level 1) of the hierarchy and continues to the base of the hierarchy (where linkage distances are short and adjacent members of the dendrogram are most self similar). At Site 8 and Site 13, Thumbi Island West, the samples at the base of the hierarchy cluster strongly by depth, implying again that the species composition at each depth is stable over time. Level 2 of the Thumbi branch separates samples from 6 and 10 m depth at Site 8 and links the 2 m samples to those of Site 13, that is 1 km away. Apparently the fauna among sites is most similar at 2 m. Similarly, for the Nakatenga branch, level 2 also joins the samples from 2 m at both sites (500 m apart) and separates them from the deeper samples at both sites. Unlike Level 3 of the Thumbi branch, the same level for Nakatenga clusters samples at 10 m across sites, of which the other cluster is mainly samples from 6 m divided by site. Apparently, the strong spatial structuring of the mbuna composition evident at Thumbi Island West within and between sites is somewhat reduced at Nakatenga Island. The species sampled at both Islands are listed in Appendix A.

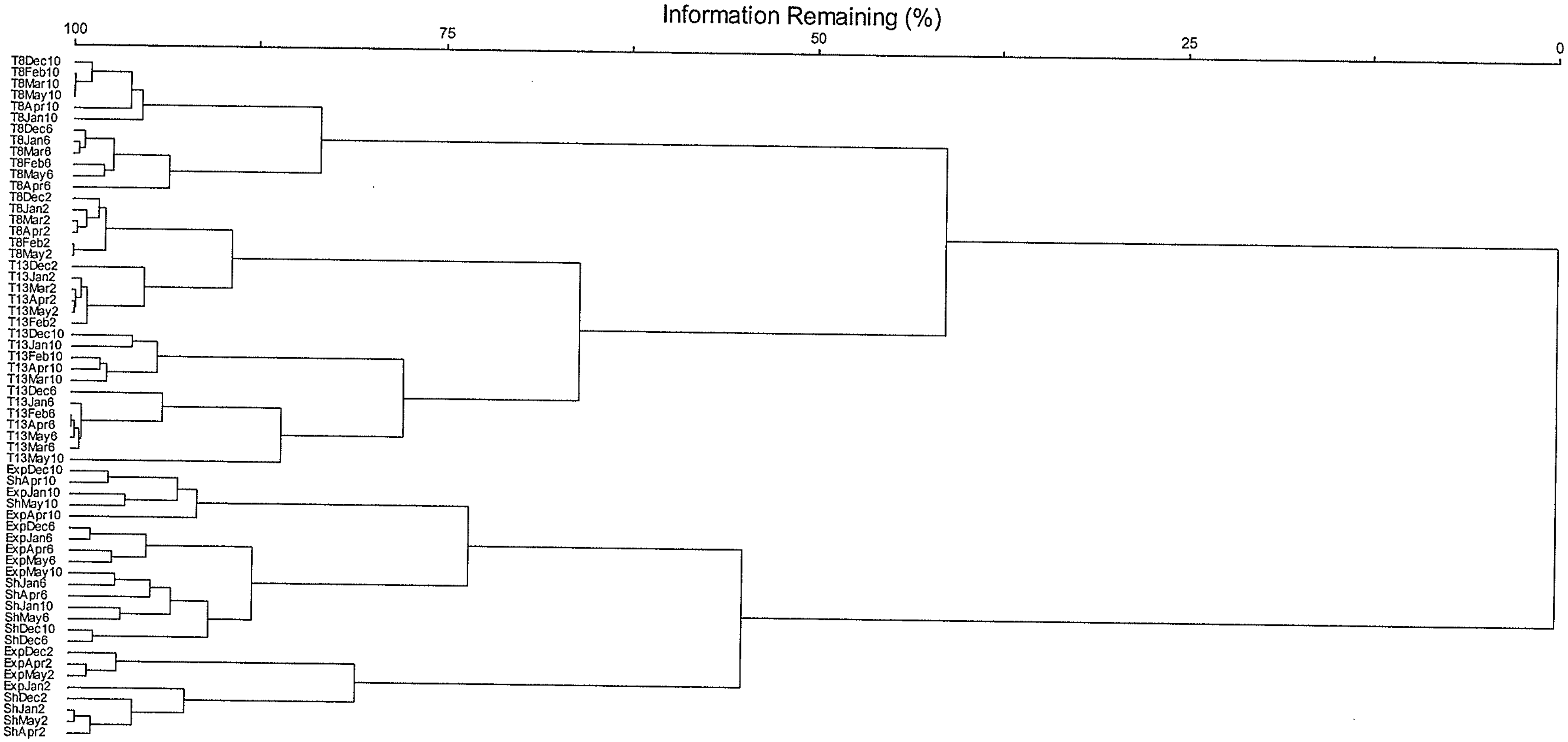

Figure 6.3. Hierarchical clustering dendrogram showing the hierarchy of relationships among species composition for rocky sites sampled at one month intervals from December 98 to May 99 at 2, 6, and 10 m depth, Thumbi Island West and Nakatenga Island. Site names are concatenated using site name, month, and depth as follows: Thumbi (T), site (8, 13), Nakatenga (Exp, Sh). Time of sample is listed by the first three letters of the month each sample was collected and is followed by depth.

6.3.2 *Sandy Shore Haplochromines*

The CA plot of the sandy shore haplochromines shows limited pattern and provides a strong contrast to the mbuna; the sandy study sites are grouped centrally in the plot and 100 of the species scores are located peripherally (Figure 6.4). Four CCA analyses were employed to assist in interpretation of the species and site scores, after removing outlier samples at 10 m from July and August (7 species). Due to the close proximity of these sites to sediment plumes during the rainy season and highly uneven distribution of individuals among species, the analyses investigated the potential influence of TSS as a constraining environmental variable and also the patterns observed for abundant and rare species. The species sampled are found in Appendix B.

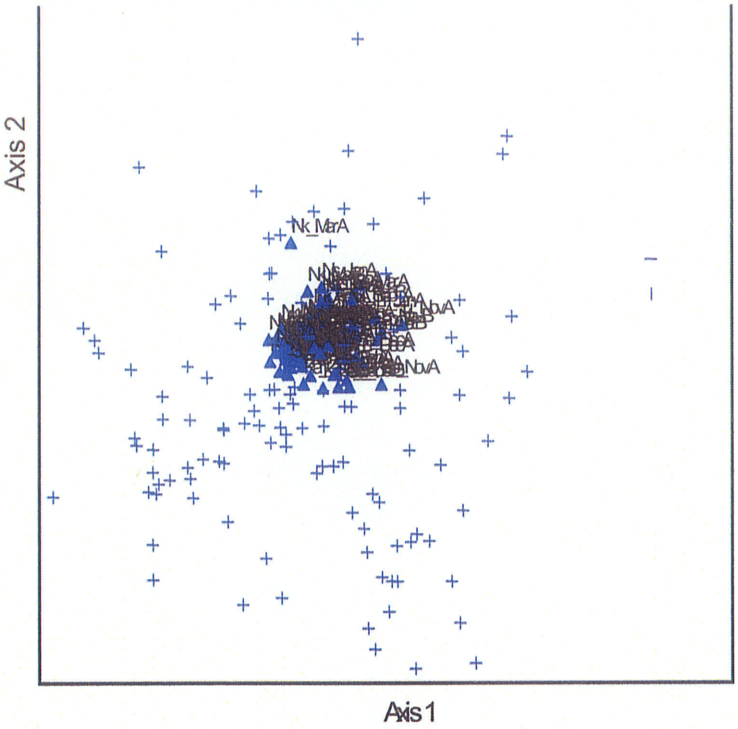

Figure 6.4. CA ordination plot showing the scores for species (crosses) and sites (triangles) for sandy shore haplochromine cichlids at 5 sites along a 28 km of the west coast of the southern basin.

6.3.2.1 *The Sandy Shore Variables*

6.3.2.1.1 *Space/Time/TSS*

The environmental gradients extracted for the sandy shore cichlids are short, as is evident by small eigenvalues (Table 6.3), and the amount of variance in the species attributed to the environmental gradients is limited. Table 6.4 shows the first axis is Space, the second is Time, and when included, TSS represents axis 3. TSS showed the smallest eigenvalue of the variables, and explained just 1.5% of the variance. The ordination improved when TSS was excluded; this is evident as a 3x increase in the variance explained by the unconstrained 3rd axis. The variance attributed to TSS in the pooled and abundant species analyses was similar; for the latter the eigenvalues and correlations are lower. The role of TSS in affecting the species composition of sandy shore fishes apparently is limited and is not considered further.

Table 6.3. Eigenvalues, species-environment correlations, and % variance accounted for by each axis, for 3 CCA axes derived from shallow sandy shore haplochromine surveys conducted at biweekly intervals from September 1998 – May 1999. λ = eigenvalue, *r* = species environment correlation, % = percent variance explained in species data.

		Axis 1	Axis 2	Axis 3
Space Time TSS	λ	0.159	0.125	0.079
	r	0.875	0.854	0.778
	%	3	2.4	1.5
Space Time TSS (abundant)	λ	0.11	0.039	0.019
	r	0.801	0.609	0.512
	%	8.9	3.1	1.5
Space Time	λ	0.159	0.125	0.234
	r	0.876	0.854	0
	%	3	2.4	4.4
Space-Time (abundant)	λ	0.110	0.037	0.141
	r	0.801	0.658	0
	%	8.9	3	23.4

Table 6.4. Canonical coefficients and interset correlation coefficients from four CCA analyses constrained to 2 or 3 variables for the pooled and abundant shallow sandy shore haplochromine cichlids.

		Canonical coefficients			Correlation coefficients		
	Axis	1	2	3	1	2	3
Space Time TSS	Space	-1.010	-0.128	0.308	-0.859	-0.159	-0.037
	Time	0.210	-0.985	-0.471	0.112	-0.847	0.006
	TSS	-0.056	0.002	1.156	0.274	-0.303	0.685
Space Time TSS (abundant)	Space	0.995	0.222	0.303	0.785	0.123	-0.026
	Time	-0.203	0.834	-0.702	-0.112	0.625	-0.110
	TSS	0.011	0.285	1.120	-0.283	0.358	0.342
Space Time	Space	0.964	-0.278	-	-0.860	-0.159	-
	Time	-0.352	-0.939	-	0.112	-0.847	-
Space-Time (abundant)	Space	0.992	0.141	-	0.785	0.131	-
	Time	-0.199	0.982	-	-0.113	0.651	-

6.3.2.1.2 Space/Time

When the Space-Time and Space-Time (abundant) analyses are compared (Table 6.3) the environmental gradients extracted from the abundant species analysis are shorter than those evident in the pooled data, and the eigenvalues are similar for Space and the unconstrained 3rd axis. In contrast, the eigenvalue of Time in the abundant species CCA diminished appreciably (a decrease of 70%) between these two treatments. This implies the abundant species are ubiquitous (i.e. widespread in space and time).

6.3.2.2 Horizontal Distribution of Species

6.3.2.1.3 Rare and Abundant Species

To visualize the distribution of the rare and ubiquitous sandy shore fishes in Space and Time, the CCA species scores were classified according to total abundance (Figure 6.5). Rare species (abundance ≤ 10) are scattered throughout the plot and so appear to be distributed randomly with respect to Space and Time. In contrast, the species scores of abundant cichlids (abundance ≥ 50) tend to be central in the plot (i.e. grouped around the grand mean of the environmental variables). Do the abundant species have preference for the middle of the coastline during the middle of the sampling period? Review of the data matrices confirmed that this is not the case. Of the 22 species classified as abundant, all but 3 species were sampled at all 5 sites. The 21 moderately abundant species (abundance 11 – 50) occurred from 1 site to 5. None of the 107 rare species were found at all 5 sites. Three rare species were observed at 4 sites, and 12 rare species were found at 3 sites.

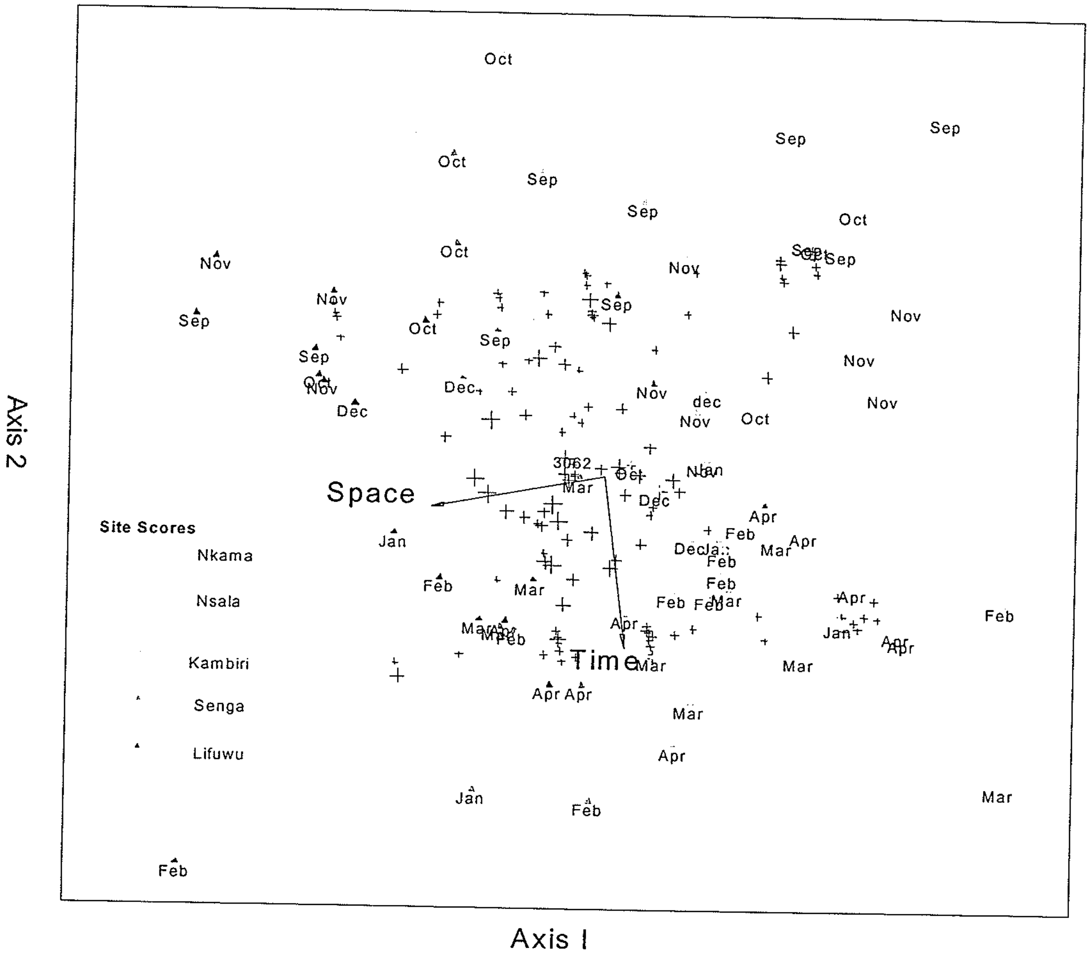

Figure 6.5. CCA species scores (crosses) and site scores (triangles) of sandy shore haplochromines. Increasing cross size indicates increasing total abundance. Each site score is labeled with the month of sampling.

Considering that the position of each species in the CCA plot is the weighted mean position along the environmental variables; this ranges from thousands of observations for the most abundant species to, at the extreme case, a single observation of a species in Space and Time. Hence, many rare species found on the sandy shores have been observed just once; this is most evident for those located peripherally around the plot (these points provide relatively less weight to the ordination). The total amount of variance explained was greatest (35%) on the abundant species analysis, and the unconstrained 3rd axis described about 23% of the variance of the abundant species (Table 6.3). This is not a surprise given redundancy in this part of the assemblage is highest and the noise due to rare species is reduced.

6.3.3 Offshore Haplochromines

It can be shown the CA and CCA results were visually identical. The CCA results show a clear grouping of deep water species (75, 100, 125 m) and sites that are clearly separated from those less than 75 m (10, 30, 50 m) (Figure 6.6). The hierarchical clustering of the offshore haplochromines provides support for the multivariate results by showing clearly the same principal division between 50 m and 75 m (Figure 6.7). In addition, most of the samples in each of these two main groups are clustered by depth, except most notably in the relatively shallow samples where samples are also clustered by Time (i.e. samples from 10 and 30 m depth strata are joined as clusters at similar times of the year). These results confirm changes in the composition of the assemblage noted in the 50 – 75 m zone, noted first by Tomasson and Banda (1996) in the Southeast arm (SE Arm), and briefly by Duponchelle and Ribbink (2003) in the SW Arm.

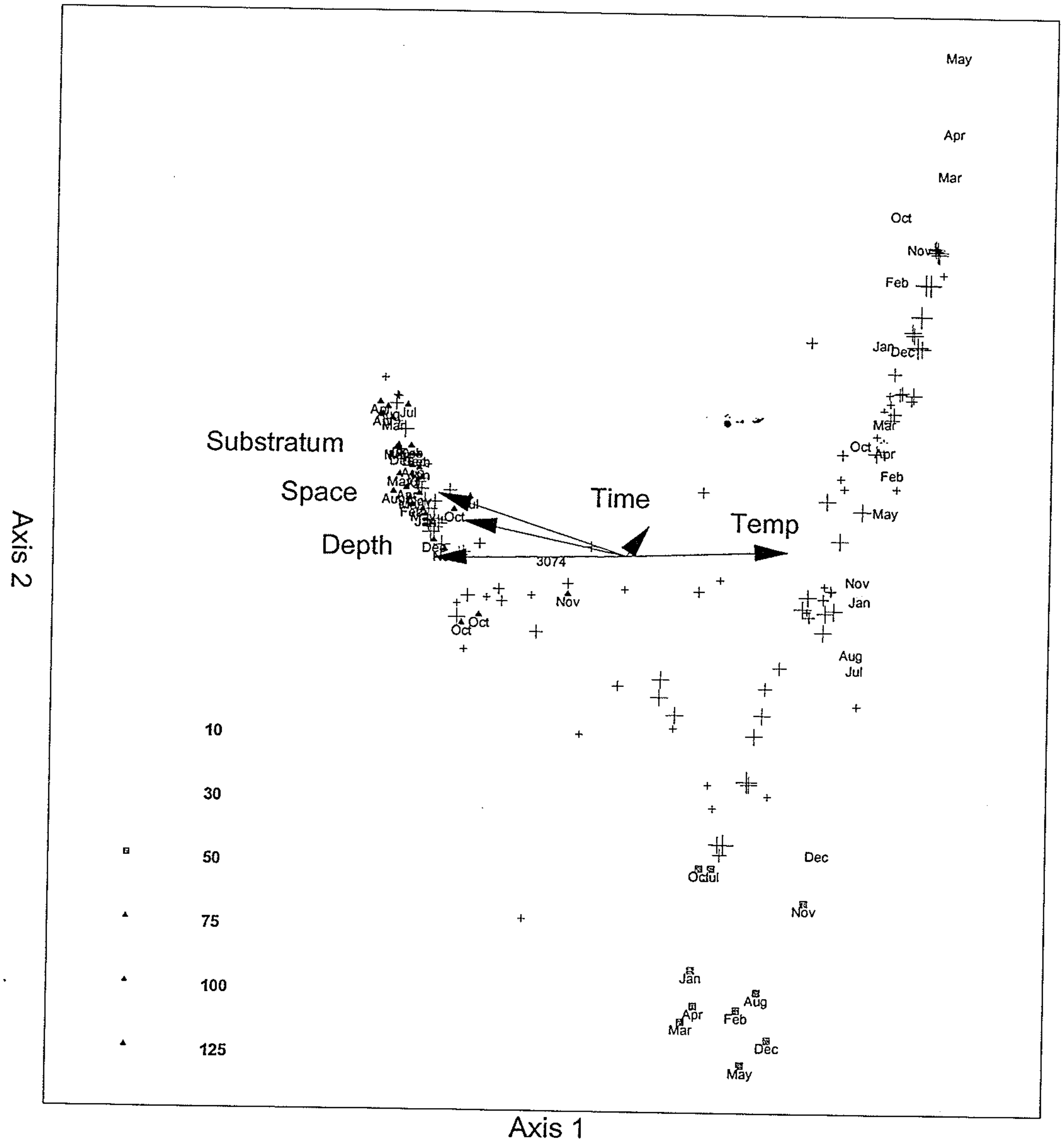

Figure 6.6. CCA species scores (crosses) and site scores (other symbols) of the offshore haplochromines collected by bottom trawling at 10, 30, 50, 75, 100, and 125 m at monthly intervals. Increasing cross size indicates increasing total abundance. Each site score is labeled with the month of sampling.

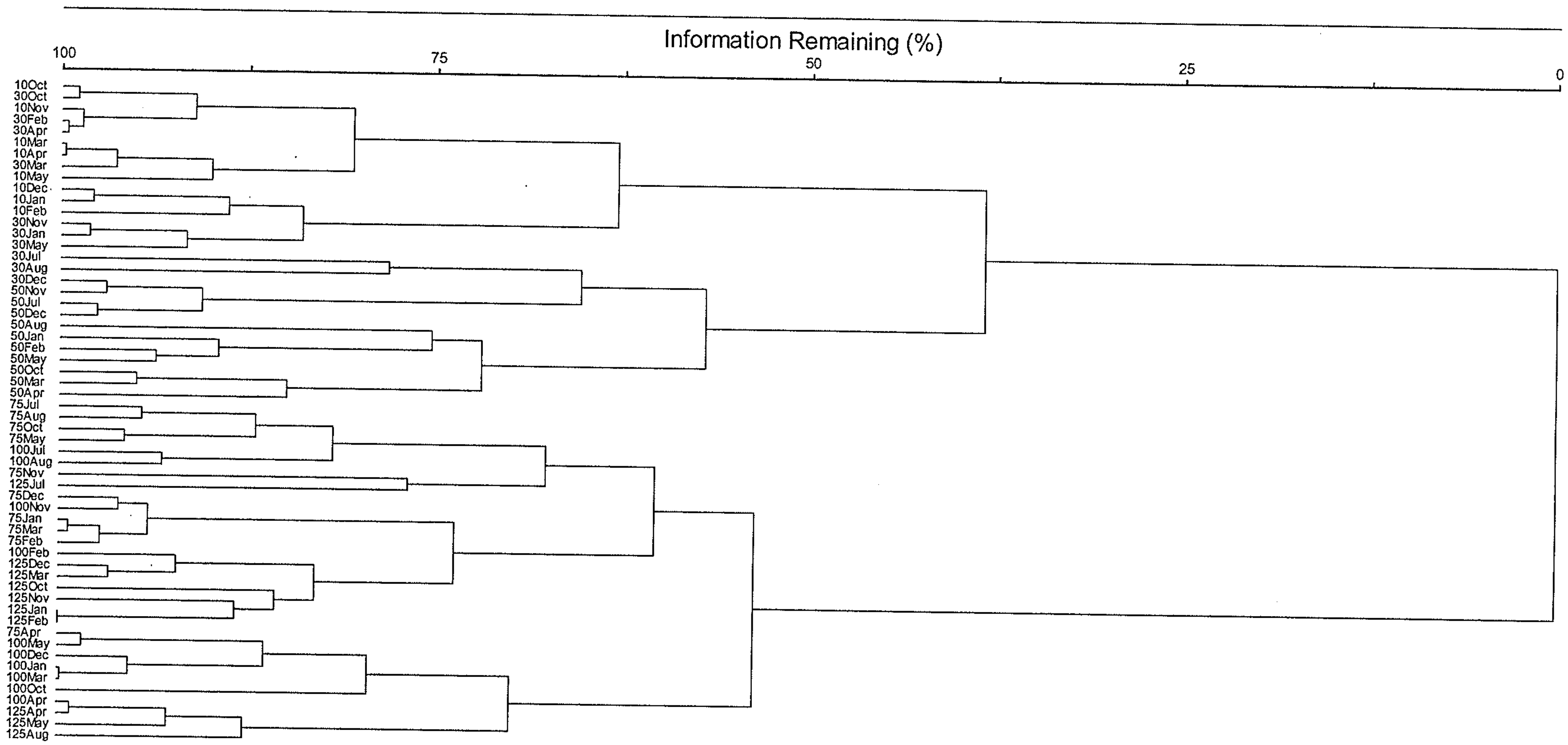

Figure 6.7. Dendrogram showing the hierarchy of relationships among species composition for 6 offshore depths sampled monthly from June 1998 to May 1999 representing 10 – 125 m water depth. Site names are listed by depth and the first three letters of the month ea each sample was collected.

The arch effect (Gauch 1982) is present in the CA and CCA results and is a mathematical artifact that arises when taxonomic composition changes along an single environmental gradient (Legendre and Legendre 2003) in which the first axis can order correctly the change in species composition amongst sites. The arch arises because the second axis carries the statistical requirement of independence of the first, so the first axis becomes folded due to differences in composition, in this case, in deep and shallow water. Palmer (1993) contends that unlike CA, a CCA will not generally create an artificial arch effect but will show one if it really exists. The similarity between the CA and CCA results and the presence of an arch confirm a major gradient in species composition is present and imply the environmental variables employed in the analysis include those that are mainly responsible for the main structure of the species data.

6.3.3.1 The Offshore Variables

The first axis of the CCA shows that Depth, Substratum, and Space are correlated (Table 6.5), and are inversely correlated with the mean water Temperature (within 20 m of the bottom). The canonical coefficients show that axis 1 is derived mainly from Depth and Substratum, axis 2 represents Space and Substratum, and the Time variable contributed most to axis 3. Nearly 30% of the variance in the data is explained. The eigenvalues show that the extracted environmental gradients range from long (axis 1) to short (axis 3) (Table 6.6). Like that shown for the sandy shore haplochromines, the influence of TSS appears limited. Removal of the TSS variable did not change the amount of variance explained, nor were marked changes evident in the eigenvalues or correlation structure (not shown). Interestingly, the CCA species scores in Figure 6.6 are not positioned close to the 50 m site scores suggesting the species found in this zone tend to have the centers of their distributions above or below this depth.

Table 6.5. Canonical coefficients and interset correlation coefficients for 120 offshore haplochromine species collected using benthic trawling at 6 depths ranging 10 – 125 m water depth on a monthly basis during a one year period.

	Canonical coefficients			Correlation coefficients		
Axis	1	2	3	1	2	3
Depth	-1.130	-3.903	0.312	-0.918	-0.016	0.112
Space	0.497	2.981	0.278	-0.767	0.138	0.202
Time	-0.046	-0.042	0.981	0.072	0.091	0.751
Substratum	-0.344	1.435	-0.424	-0.889	0.259	-0.112
Temperature	0.030	-0.026	0.072	0.732	0.043	0.201
TSS	0.045	0.090	-0.150	0.005	0.109	0.359

Table 6.6. Eigenvalues, % variance accounted for by each axis, and species-environment correlations from a CCA for the offshore haplochromine species. .λ = eigenvalue, r = species environment correlation, % = percent variance explained in species data.

	Axis 1	Axis 2	Axis 3
λ	0.778	0.311	0.107
r	0.982	0.852	0.836
%	19.3	7.7	2.6

To better understand the haplochromines unique to the shallow and deep water settings and to contrast the influence of the Space and Time variables, two CCA's were run using the abundance–based reclassification method. The trawl data were partitioned into three groups: Unique shallow (≤ 50 m), Unique deep (≥ 75 m), and Unique Shallow

+ Deep. The analysis first used Depth, Space, and Time, which then was compared to the Depth and Time trial to assess the importance of the Space variable. The Substratum, Temperature, and TSS variables were excluded because partitioning of the data into shallow and deep groups is coincident with the major sand/mud boundary, diminishes the temperature gradient appreciably, and our estimates of TSS throughout the study were low (about 1 mg/l). This concentration is near the lower threshold of making a meaningful TSS estimate with these data (G. McCullough, University of Manitoba, Pers. Com).

6.3.3.1.1 Depth/Space/Time

The eigenvalues of the species unique to shallow water are markedly larger than those extracted from the unique deep and shallow + deep groups, except for axis 1 of Unique Shallow + Deep (Table 6.7), implying either long or short environmental gradients are present. All three axes of the Unique Deep group demonstrate short gradients, as do axis 2 and 3 of the Unique Shallow + Deep group. Table 6.8 shows axis 1 is derived from Depth and Space, axis 2 is a combination of residuals of axis 1, and axis 3 is Time. Interset correlations are similar between Depth and Space except for Unique Shallow + Deep where correlations of Depth were higher. Species environment correlations are high, and remain so after the Space variable was removed.

Table 6.7. Comparison of results of CCA ordinations of offshore haplochromine data partitioned into the three groups: 1) fishes unique to the shallow group (< 75 m), 2) fishes unique to the deep group (> 50 m), and 3) the remaining fishes found in one or more depth strata in both of the shallow and deep groups. No. of Vars = 3 represents the CCA analyses using depth, Space, and Time. No. of Vars = 2 represents the CCA analyses using depth and Time. λ = eigenvalue, r = species environment correlation, % = percent variance explained in species data.

	No. Vars.		Axis 1	Axis 2	Axis 3
Unique Shallow (< 75 m)	3	λ	0.748	0.245	0.235
		r	0.976	0.843	0.852
		%	20.1	6.6	6.3
	2	λ	0.658	0.238	0.47
		r	0.934	0.799	–
		%	17.7	6.4	12.6
Unique Deep (> 50 m)	3	λ	0.116	0.094	0.067
		r	0.804	0.865	0.706
		%	8.5	6.9	4.9
	2	λ	0.111	0.093	0.234
		r	0.813	0.852	–
		%	8.1	6.8	17.1
Shallow + Deep	3	λ	0.584	0.076	0.049
		r	0.941	0.761	0.705
		%	26.9	3.5	2.2
	2	λ	0.522	0.049	0.271
		r	0.891	0.709	–
		%	24	2.2	12.5

Table 6.8. Comparison of canonical coefficients and interset correlation coefficients for 120 offshore haplochromine species partitioned into three groups by depth and analyzed using Depth, Space, and Time (No. Vars. = 3) or depth and Time (No. Vars = 2).

	No. Vars.		Canonical coefficients			Correlation coefficients		
		Axis	1	2	3	1	2	3
Unique Shallow (< 75 m)	3	Depth	3.302	-7.901	-5.223	-0.884	-0.279	-0.224
		Space	-4.239	7.512	5.140	-0.921	-0.212	-0.184
		Time	-0.055	-0.536	0.864	0.132	-0.427	0.726
	2	Depth	-1.006	-0.147	–	-0.933	0.028	–
		Time	-0.035	-1.016	–	0.135	-0.790	–
Unique Deep (> 50 m)	3	Depth	-11.301	-3.542	-30.453	-0.702	0.365	0.171
		Space	10.457	4.021	30.701	-0.695	0.366	0.192
		Time	-0.396	-0.911	0.158	-0.337	-0.754	0.181
	2	Depth	0.925	0.385	–	0.769	0.278	–
		Time	0.327	-0.947	–	0.312	-0.787	–
Shallow + Deep	3	Depth	1.871	-2.151	0.049	0.880	0.265	-0.041
		Space	-0.997	2.669	-0.077	0.710	0.499	-0.032
		Time	0.063	-0.003	1.000	0.012	0.026	0.704
	2	Depth	1.000	0.014	–	0.890	0.034	–
		Time	0.048	-0.999	–	0.013	-0.709	–

6.3.3.1.2 Depth/Time

Constraining the CCA to Depth and Time provided in a shift of the Time variable to axis 2. In all cases, removal of the Space variable increased the total amount of variance explained, largely by increases of the unconstrained 3rd axis; this is most notable for the Unique Deep group as a 12 % increase. The eigenvalues and species environment correlations for both trials in Table 6.7 remained similar for axis 1. Removal of the Space variable resulted in decreases in the explained variance of axis 1 of about 3% for Unique Shallow and Unique Shallow + Deep. In contrast, a decrease of about 0.4% for the Unique Deep group suggests the importance of Space as an evolutionary gradient in deep water is limited.

6.3.3.2 Vertical Distribution of Species

Of the 120 offshore species studied, only 8 species were found at all six depths. Sixty species were unique to the depths ≤ 50 m. In contrast, only 22 species were unique to depths ≥ 75 m. The remaining 38 species were present in one or more of the depth strata in both the shallow and deep groups.

6.3.3.2.1 Richness

The richness of the species unique to the zone above the mud boundary decreases with an increase in water depth. At 10, 30, and 50 m depth intervals 44, 41, and 20 species were observed. Thirty species were present in the 10 – 30 m depth strata whereas 13 species were found at 30 and 50 m. In contrast, the species number unique to the zone below the mud boundary (75 m – 125 m) ranged from 13 – 17 across depths and 11 of the 22 species found only in this zone were found across all three depths.

6.3.3.2.2 Rare and Abundant Species

The number of rare species in the Unique Shallow group is highest in the 10 – 30 m depth range, and decreases markedly with an increase of water depth, as shown in the CCA results (constrained to Time and Depth) in Figure 6.8. Sixteen rare species were sampled in the sandy shallow zone at or above 50m. The number of rare species at the 10, 30, and 50 m sampling sites was 12, 7, and 4, respectively. Only 2 rare species were present below 50 m.

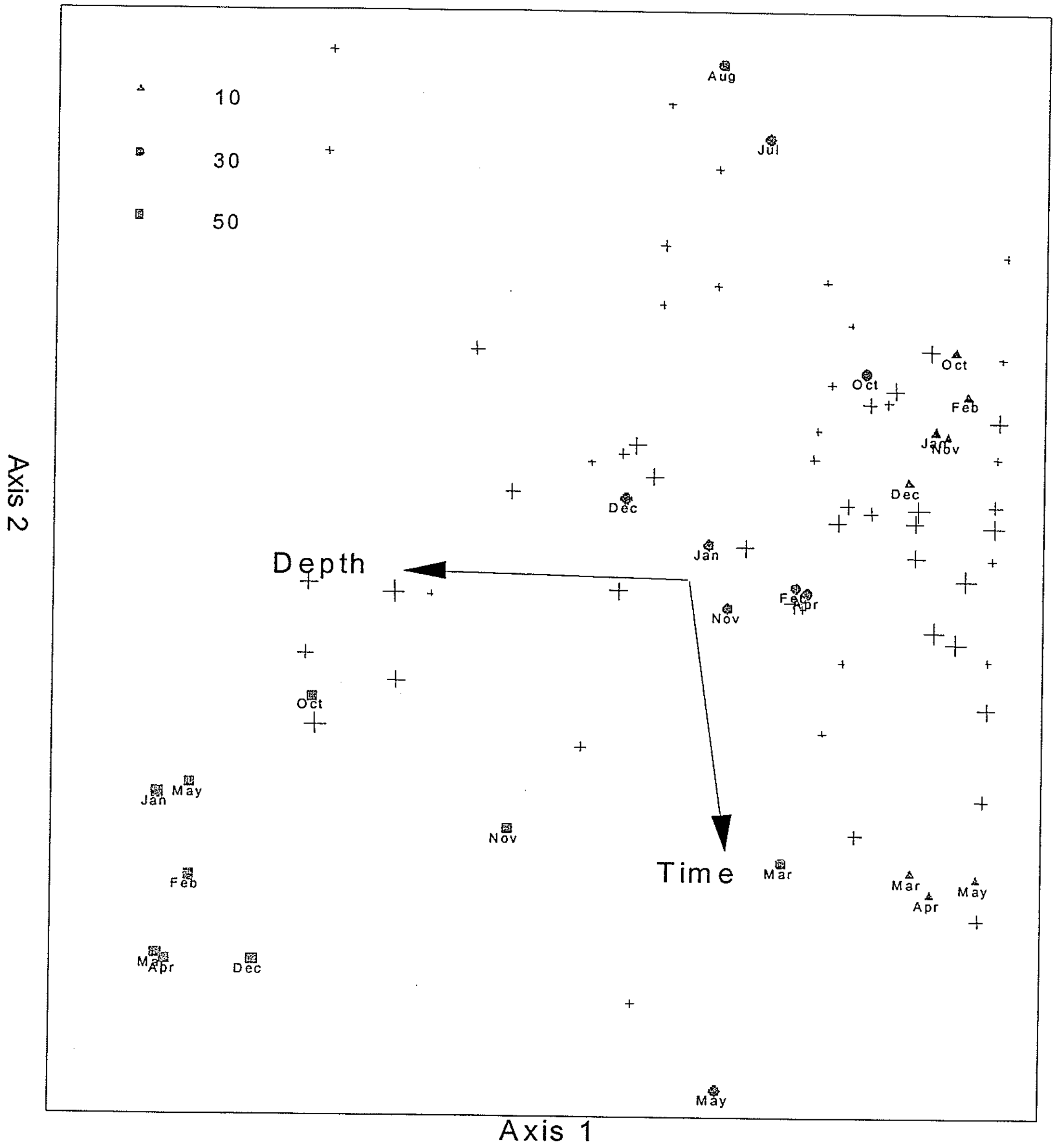

Figure 6.8. CCA ordination of 60 species of offshore haplochromine species unique to water less than 75 m, constrained to Depth and Time. Increasing cross size indicates increasing total abundance. Site scores are symbolized and show shallow water is on the right side of the figure. Site scores are shown in the legend.

All three groups evident in the trawl samples have abundant species. The abundant species in the Unique Shallow and Deep groups (not shown) sampled at all depths generally are located in the center of the plot, and imply ubiquity. In the shallow group, the abundant species found at two of the three depths are centered with a preference for water less than 30m. In the deep group, many species show a strong central (i.e. ubiquitous) distribution in Space and Time. Few species have centers of their distributions along the periphery of the plot.

Most of the species of the Shallow + Deep group (i.e. 24 of 38) have centers of their distributions in water depths less than 50m (9 species) or greater than 75m (15 species), and like the fishes unique to either deep or shallow water, a preference is shown for either the shallow sandy zone or the deep muddy one. The species of the Unique Shallow + Deep group frequently cross the 50 – 75 m zone, but the frequency of observation of each species drops markedly after the boundary is crossed (Appendix C).

In summary, 106 of 120 (88%) species studied showed preference either for shallow water and sandy bottom or a deep water zone where deposition dominates. More than 2/3 of the species (i.e. 82 species (68%)) showed an abrupt discontinuity in distribution on either side of the 50 – 75 m depth zone where the mud boundary was observed.

6.4 Conclusions

Two main research questions were addressed in this chapter. The first was: 1) Do habitat discontinuities at local scales influence species composition, and is there evidence to suggest that ephemeral changes in the environment cause seasonal shifts in the composition? This question is designed to illustrate if the boundaries of conservation or management units could be perceived to be static, or need to change within the year. The second question was: 2) What are the relative roles of evolutionary and environmental variables that account for variation in the species data? This question addresses the same theme but in the quantitative sense, and emphasizes the need to understand the influences of evolutionary variables such as Space (i.e. distance) and Time. The improved understanding provided by addressing this question could help to assess the relative size for any conservation or management zones, and to understand if the composition within any such zone could be perceived to be static or might change within the year.

Both research questions were addressed using multivariate methods and a hierarchical clustering technique for each of the datasets. The results supporting the first question show clearly that species composition at is strongly influenced by habitat discontinuities that are temporally invariant, like substratum boundaries, rather than ephemeral variables such as temperature or TSS. This chapter has shown that three main assemblages can be distinguished using habitat distributions. The finding that the mbuna species composition changes from island to island is not new, but the dramatic change in species composition of the haplochromines between 50 – 75m that is coincident with the zone of the sand/mud boundary is.

The variables subject to multivariate analysis in this chapter to address the second question were: Space, Time, Depth, TSS, and water Temperature (within 20 m of the bottom). These multivariate analyses provide a novel quantitative assessment of the relative importance of Space, Depth and Time for each of the rock shore, sandy shore, and offshore data. The composition of mbuna species is influenced mainly by Space and Depth, which accounts for 31% (67% of the explained variance) and 15% of the total variance, respectively. Subsequent study of the mbuna on the mainland or other islands could show that Space to be slightly less pronounced. In this study our island samples may have a higher degree of isolation than mainland stretches of coast (i.e. higher endemism), and the translocation of 5 species to the 35 (Ribbink et al. 1983) species that inhabit Thumbi West Island could elevate the differences in composition between islands. The limited role of Time in the CCA analyses (0.4% variance) suggested the species composition is temporally invariant, at least up to about 0. 5 yr. The strong hierarchical clustering of mbuna data by site and depth at Thumbi West Island reinforces this conclusion.

The importance of Space on describing differences in the species composition appears to be limited for the sandy shore (< 9%) and offshore fishes (0.4 - 3%), but is especially important for those unique to deep water (≥75m). When compared to the mbuna, the 23 km of distance between rocky habitats of isolated island habitats confirm marked differences in the composition of the mbuna assemblages. The sandy shore and offshore sampling sites range nearly 2x farther, but do not demonstrate similarly strong contrasts in species composition due to Space alone. The sandy shore species in high abundance were widespread and differences in assemblage composition from site to site are due mainly to rarity, which is extreme in shallow water, and appears to be distributed randomly in Space and Time. Time explained little variance for the mbuna but increased about 8x for the sandy shore (3.1%), and 17x for the offshore samples (6.9%). Rarity of the sandy shore samples probably is elevated due to fish harvests in the area (Sululu 2000), but still reasonably extends the trend evident in the demersal trawls of increasing rarity as water depth decreases. When the species lists from the smooth bottomed habitats were compared to those of Turner (1996) for the SW arm and Snoeks (2001), it is evident that while many species in our sandy shore samples are unique to sites, they are not endemic to this study area. The present shallow sandy sites and the offshore sites up to 50 m depth, therefore, appear to have sampled fishes that are a part of a much larger, but peripherally distributed, biogeographic pool.

The offshore demersal trawl samples are divided into shallow and deep water haplochromine assemblages by an apparent major environmental gradient that results from one or a combination of Depth, Substratum, and Space; all three variables are correlated and so are difficult to separate unambiguously. However, all analysis methods grouped clearly the species of the 75 m trawl site with deeper sites that range 30 km, even though the 50 m and 75 m sites are only 3.5 km apart. Space appears to be the least important of the correlated variables. Indeed, the species complementarity of these deep water (75m +) sites is high, about 70%, which is exceeded only by the similarity in species found between the 10 and 30 m sites (82%)(P. Cooley, unpublished data). Also, the fact that excluding the Space variable from the offshore CCA analysis had little effect on the species environment correlations and canonical coefficients suggests a limited influence (see Ter Braak 1986). This also rules out the possibility that depth may be more important in the nearshore zone and Space more important in the offshore zone.

The effects of temperature and TSS on the species composition of the present data appears limited. It is important to note that our surveys were designed to collect baseline data, and the effects of sediment was a corollary focus. New insight into the temporal dynamics of the Linthipe River has been gained as result of another Ph.D. thesis in progress. It is now apparent that the present monthly samples are not instep with the temporal dynamics of the TSS regime that varies diurnally. The present analyses should be considered preliminary and used as a stepping stone to more focused study of the effects of sediment on the haplochromines.

The differences observed between the hierarchical clustering of the mbuna between Thumbi West (no sediment) and Nakatenga (sedimented) suggests that increased sediment reduces the spatial structuring (distribution of species composition by site and depth) which was strong at Thumbi West but was weaker at Nakatenga. Unfortunately, no other studies exist to either confirm or deny this pattern. It remains uncertain if the greater apparent similarity between sites and depth strata at Nakatenga is attributed to sediment, or is an artifact that resulted due to closer proximity of the sites at Nakatenga.

6.4.1 Summary

Direct comparison of the rock shore, sandy shore, and offshore fishes is difficult due to biases that accompany different methods of data collection that are essential to sample a wide range of depth and bottom types. The methods used here are considered a best practices approach and can be expected from similar studies in the future. The CCA method does not infer cause and effect, but the analytical approach using direct gradient analysis (CCA) with methods that assess pattern only in the biological data (i.e. indirect gradient analysis and hierarchical clustering) provide strong support in defense of the variables used in the constrained method.

This study benefits from an extensive temporal sampling and large sample sizes that more fully characterize the assemblages when compared to single point in time samples. Each of the three study areas studies has also a similar range in distance, 24 km (mbuna), 28 km (sandy shore), and 37 km (offshore) that facilitate qualitative comparison. Detailed contrasts are difficult because of different spacing of sites within each dataset, and differences of sampling period, and interval. Fortunately, the trends that showed high spatial structuring and low changes in species over time were derived from the samples fewest in number and collected during the shortest time span; this appears to preclude any confounding effects due to variable sampling effort over time. Also, many of the contrasts within and between each dataset are large with respect to the sampling biases and enable a combined synthesis.

Changes in species composition for the mbuna and offshore species are clear and correspond to habitat discontinuities that are stable over time. This suggests the design of parks or fisheries management zones may reasonably use static boundaries to segment the main assemblages according to distribution of rock, sand, and mud (i.e. deep water) distributions. The analyses also reveal an unmistakable dichotomy exists between the fishes inhabiting rough and smooth bottomed habitats where the importance of Space and Time as descriptors of changes in species composition appear to be inversely related. For the mbuna, Space is an important descriptor of changes in assemblage composition but Time is not. Space is a far less important descriptor of changes in composition for the haplochromines over sand and mud, and yet the importance of Time increases. This provides evidence to suggest the composition changes over time. This means the assemblages inhabiting the smooth bottomed habitats literally are a moving target for conservation. I conclude these three general habitats provide a logical basis from which to conduct future research and to design plans for conservation and management.

In conclusion, the composition of the cichlid assemblages appears to reflect persistent habitat characteristics rather than ephemeral influences, such as TSS or water temperature. The results support the widely held view that stenotopy of the mbuna is high. This dissertation provides quantitative evidence that supports the growing contention (Arnegard and Snoeks, 2001, Snoeks in press) that the stenotopy of the sandy and mud species is comparatively low. The available data suggest the importance of Space is greatest for the mbuna and least important in deep water over mud. Accordingly, the relative size of parks/management units could follow the order of small, moderate, and large for the rock, sand (0 – 50 m), and mud (50 – 125 m) assemblages, respectively.

The specific size of the units for the shallow and deep haplochromines over sand and mud is more difficult to assess than the mbuna, and requires further study.

Chapter 7 continues the study of the haplochromine datasets but the perspective shifts from biogeographic (spatial and temporal) to an ecological and temporal study now that three haplochromine assemblages have been identified associated to three main habitats, and the relative order in size of these management units has been inferred. The next chapter explores in more detail the structure and richness of these assemblages to appreciate their relative levels of richness, and examines the information contained in the accrual of richness and temporal variation of the samples.

Chapter 7 Species Accrual and Temporal Variation of Haplochromine Cichlids in Rock, Sand, and Mud Habitats of Lake Malawi

7.1 Introduction

Species diversity can be reduced to two constituents: species richness, which is the number of species in the assemblage, and species evenness, which is the relative distribution of individuals among species. Species richness is widely used measure of diversity because it is simple and easily understood by scientists, managers, and the public, is often used in the establishment of conservation priorities, and in principal can be compared across assemblages. The richness of specific assemblages however, tends to be poorly understood because species richness covaries with sample number. It is well known that the repeated observation of richness over time underestimates the richness, and so is a negatively biased approach, until the sampling effort exhausts the species pool. Scientists also know that complete sampling is a luxury rarely afforded. As a result, models for estimating richness (Colewell and Coddington 1994) have been proposed recently that try to offset that negative bias.

Colewell and Coddington's nonparametric models of species accumulation awaited trial by fire with real and simulated data sets until the late 1990's (e.g. Hellman and Fowler 1999, Thompson et al. 2003). Simulation data sets show clearly that the shape of the species accumulation curve (SAC) is dependent on community properties such as richness, abundance, and evenness (Thompson and Withers 2003), and so the slope of the initial curve is a diversity index (Kowalewski 2000). The initial rise of a SAC produced by repetitive sampling of a population results mainly from the abundant species that have a high propensity for being observed. The slope and intercept of the curve thereafter depends more on the proportion of rare species (i.e. evenness). The application to real data however has, been less convincing. Comparisons across habitats or populations are difficult due to interaction by properties of the assemblage, choice of model, sample size, and uncertainty about the sampling frame (i.e. habitat unit) and taxonomic boundaries of an assemblage. The present haplochromine data potentially are suited for such comparisons because, as shown in Chapters 4, 5, and 6, the temporal samples are exceptionally large and demonstrate clearly that habitat discontinuities frequently are abrupt and result in marked changes in species composition.

Site richness is a cornerstone for many conservation efforts. Rare species are characteristic of species rich sites (Hubbel 1997), and contribute to total site richness, but are infrequently encountered. If the total cumulative species richness can be observed or estimated is it appropriate that such a value be considered static and unchanging? Clearly, different assemblages could attain a similar total richness but may be structured quite differently. It also has been argued reasonably that diversity indices that combine all information on occurrence and relative abundance for all species are difficult to interpret (Peet 1975), and their potential for providing useful insights into conservation and management has been questioned (for review see Magurran 1988). How can the eveness, relative abundance, and richness be summarized to readily convey differences among assemblages without the undesirable abstraction that results with diversity indices?

Identifying biodiversity "hotspots" is a common notion in conservation biology. This process indirectly creates an ordinal ranking against other sites of lower richness. An ordinal ranking of low, moderate, and high areas of species richness in a rich and vast system such as Lake Malawi could provide a convenient way to prioritize areas for conservation efforts. It has already been shown in Chapter 6 the three main habitats have almost entirely different species compositions. Can the species richness of rock, sand, and mud (i.e. deep water) species be ranked in an attempt to prioritize areas for conservation planning?

This dissertation has already shown that three largely unique assemblages can be inferred by the distribution of physical habitat. Chapters 4 and 5 showed the horizontal and vertical discontinuities in habitat over the full range in Space and a wide range in Depth, and showed that the mbuna composition of the mainland coast mirrors the tectonic framework of the basin. A focus of Chapter 6, the previous chapter, was to assess the spatial differences in species composition and new light was shed on the largely different assemblages found in shallow water over sand, and in deep water over mud. Evidence therefore is strong to suggest the geometric shape of habitat distributions reflects species ranges at the level of the assemblage.

In this chapter I examine the cumulative levels of richness, rarity, and the temporal variation of the rock, sand, and mud (i.e. deep water) assemblages. Because richness may not differ between these assemblages I also investigate the temporal variation of the assemblages to see if that information provides additional ecological information to assess differences among groups.

This information is important because it sets synoptic one-time surveys, which are the norm and not the exception on this large lake, into an appropriate context in terms of sampling completeness. Given that the shape of a SAC also conveys information about the structure of assemblages, comparison of the accrual of fishes inhabiting rock, sand, and mud habitats could provide graphical insight (i.e. easy to interpret) into understanding assemblages structure in addition to richness. This chapter investigates the following research questions for the rock, sand, and mud (i.e. deep water) assemblages:

1) *How many sampling events are required to sample sufficiently each of these assemblages?*

2) *Can one model of species accumulation be applied equally well on all groups?*

3) *Does the frequency of presence and abundance by species vary in the groups or is it unchanging?*

4) *Can the species richness of rock, sand, and mud (i.e. deep water) habitats be reduced to ordinal classes to infer the ranking of areas for conservation priorities?*

These questions direct a study of species accrual and an examination of temporal variation. The first question requires implementation of a series of species accumulation models and an assessment of their bias, precision, and accuracy. The first point also requires the asymptote or "ceiling" of richness be defined by the model(s) so effort on the abscissa can be defined unambiguously. Use of a single model across assemblages, point 2 above, is important because differences in shape of the curve reflect properties of the assemblage, not differences due to model design. Question 3 also is important because the accrual of species over time is cumulative; the total species number cannot convey potentially important information about the temporal variation that occurs during the accrual. This point is key because an assemblage with a high variation suggests a mobile character, and confounds the concept of site richness as a conservation strategy. The last point compares the richness across assemblages but carries the important caveat that sampling must be complete across groups.

7.2 Methods

7.2.1 Data

This chapter continues the study of the haplochromine data presented in Chapter 6 and introduces new haplochromine data for the non-mbuna at the rocky island sample sites.

7.2.2 Species Accrual

To yield statistical estimates of species richness I implemented 8 estimators based on a randomization procedure that operated on a species-by-sample data matrix populated with either incidence (i.e. presence/absence) or abundance data. Randomization of sample order produces a smoother curve that simplifies comparison because field data tend to accumulate species with random sampling error. The models are described in detail by Colwell and Coddington, (1994), Colwell (1997), and Chazdon (1998). The incidence based estimators are: Observed richness (Sobs), Incidence based Coverage Estimator (ICE), Chao2, Jacknife1 (Jack1), Jacknife 2 (Jack2), Bootstrap, Michaelis Menton Mean (MMMean). The abundance based methods are: Chao1, Abundance Based Coverage estimator (ACE). The Coleman curve (Cole) was similar to the observed (randomized), species accumulation curve (Sobs) for these data, suggesting a randomization protocol was justified. All data are treated using the full suite of models except for the non-mbuna for which incidence data were available. In each case, 100 randomizations of sample order were undertaken to construct a statistical distribution of species accumulation, from which the mean was calculated. Randomized species accumulation curves were generated using the unpublished program, EstimateS, version 6.0b1, developed by R. K. Colwell. EstimateS is available at: http://viceroy.eeb.uconn.edu/estimates.

The analyses are based on balanced (i.e. equal number) replicates within each sampling method. However, because site richness is dependent on sample number, the maximum number of samples is used to avoid the bias where data partitioning contributes to incomplete sampling, and a false conclusion regarding a non-asymptotic result. In other words, the number of SCUBA, beach seine, and trawl sample numbers were not standardized as a group prior to study.

The number of species and individuals/unit area for the samples was estimated using information from Ribbink et al (1983), Sululu (2000), and Day (1999). The mbuna SCUBA transects are 50 m^2 each, the seine net hauls each range in area from 11250 m^2 – 22500m^2, and each pass of the benthic trawl sampled on average 6622 m^2. For the seine net hauls, it was assumed the area sampled started at 80% of the total length of the seine pull, and completed at 30% of the total width.

7.2.3 Temporal Variation

To compare directly the temporal variation of the three sample groups, the datasets were standardized by selecting a common time period (December - May) and sampling interval (1 sample/month); n = 6 for each sample group, except for Nakatenga Exposed where n = 5 from October - May. From these data the average coefficient of variation (V) was determined from the abundance data, and the average frequency of occurrence, median, and modal number of transects that species were encountered at sample each site was calculated. The non-mbuna data were presence/absence and were not included in this analysis.

7.3 Results and Discussion

7.3.1 The Form of the Species Accumulation Curve:

7.3.2 Non-Mbuna and Mbuna:

The form of the species accumulation curves from rock habitats was similar for the non-mbuna and formed an asymptote but with a slight positive bias (i.e. overestimate) of the estimated richness (Figure 7.1). The suite of models overestimate richness on average at Site 8 and Site 13 by 13% and 16%, respectively (Table 7.1). The rarity statistics show that Site 8 has a higher richness and more rarity than Site 13. At Site 8, 19% of the species were observed just once, and 14 of the 17 species of non-mbuna recorded in this study were unique. At low randomized sample number Chao2, MMMean, and ICE provided unstable results.

This study was the first to document male mbuna and non-mbuna at the same time. A maximum of 59 species were recorded at Site 8 with a maximum species density (i.e. number of species/unit area) was 0.39 m^2 for the 2 – 10 m aggregate depth zone.

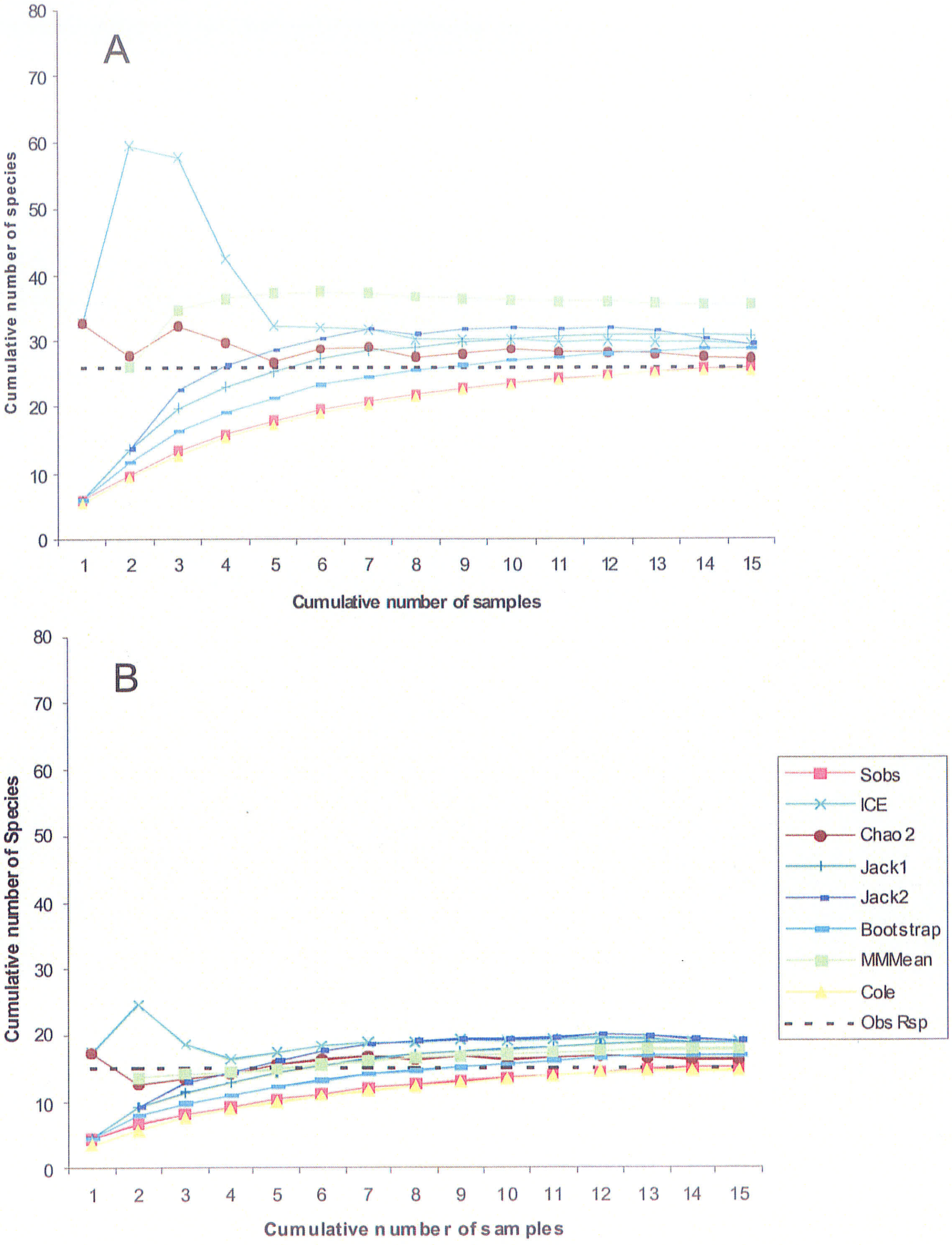

Figure 7.1. Randomized species accumulation curves for the non-mbuna from rock habitats (a) at site 8 and (b) site 13, Thumbi Island West. Full model names are listed in the text. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

Table 7.1. Estimated species richness and summary statistics of the non-mbuna from the rock littoral of Thumbi Island West. The non-mbuna data are presence/absence.

Richness Estimate	Site 8	Site 13
ICE	29.4	18.8
Chao2	27.3	16.2
Jack1	30.7	18.7
Jack2	29.4	18.9
Bootstrap	28.8	16.9
MM mean	35.3	17.9
Observed Richness	26	15
No. of samples	15	15
No. of male observations	93	58
No. of single obs.	5	5
No. of double obs.	7	3
No. of rare sp. obs. (<11)	26	15
No. of unique obs.	14	3

At Nakatenga Island, the mbuna species accumulation curves show a higher initial slope than those of the non mbuna, and after 3 – 4 samples a plateau is evident and the suite of curves converge on the observed richness (Figure 7.2). As shown in Table 7.2, the estimated and observed richness of the mbuna at Nakatenga Island is equal (error < 3%). At the larger and more speciose Thumbi Island West, the same amount of sampling effort provided a suite of non-asymptotic curves (not shown) with a positive bias that on average overestimated richness by 14%. Sampling at Thumbi Island West did not reveal an upper limit to richness as was shown for Nakatenga Island. Fortunately, this analysis can be extended to assess if and why an asymptote exists at higher sampling completeness because the sampling program at Thumbi Island began before the paired sampling program on both islands.

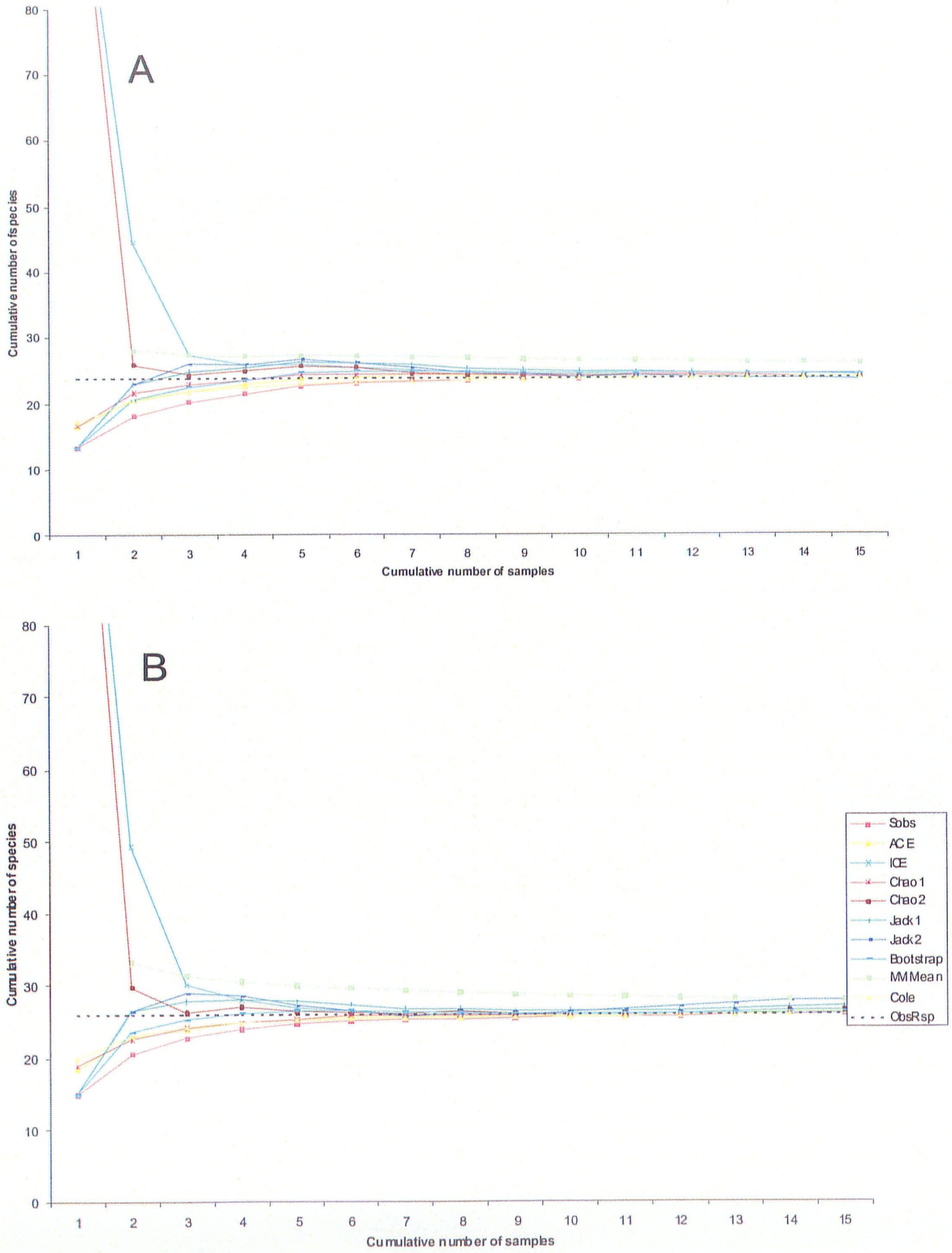

Figure 7.2. Randomized species accumulation curves for the rock dwelling mbuna at Nakatenga Island at (a) Sheltered and (b) Exposed. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

Table 7.2. Estimated species richness of the mbuna from the rock littoral of Thumbi Island West derived using 8 non-parametric models, with summary statistics describing rarity for the mbuna. The * indicates species accumulation curves and statistics generated using a larger number of samples.

Richness Estimate	Nakatenga Island		Thumbi West Island		Thumbi West Island	
	Sheltered	Exposed	Site 8	Site 13	Site 8*	Site 13*
ACE	24.0	26.3	38.6	33.8	39.1	29.6
ICE	24.0	26.2	31.4	31.9	38.9	29.4
Chao1	24.0	26.5	34.6	32.5	38.6	29.1
Chao2	24.0	26.5	34.6	41.5	41.3	29.0
Jack1	24.0	26.9	33.7	33.7	38.8	30.0
Jack2	24.0	27.8	37.1	38.0	43.4	30.0
Bootstrap	24.0	26.4	30.9	30.9	35.4	27.3
MM mean	25.6	27.9	30.3	29.8	33.0	29.6
Observed Richness	24	26	29	29	33	29
No. of samples	15	15	15	15	27	27
No. of male obs.	1660	1431	1390	1693	2605	3006
No. of singletons	0	1	5	4	5	1
No of doubletons	0	0	1	1	1	2
No. of rare sp.(<11)	4	5	9	9	10	8
No. of uniques	1	3	4	2	6	2

Nearly twice the sampling effort at Thumbi Island provided mixed results (Figure 7.3). At Site 13, randomization of the full sample resulted in a clear and marked asymptote by all models that again converged on the observed richness (mean error<1%), although the estimate of the second order Jacknife showed a slight negative bias. In contrast, about half of the models of the more speciose Site 8 reluctantly formed an asymptote near the end of sampling. A positive bias remained throughout the curve and overestimated richness again by 14%. At low randomized sample number Chao2 and ICE provided unstable results.

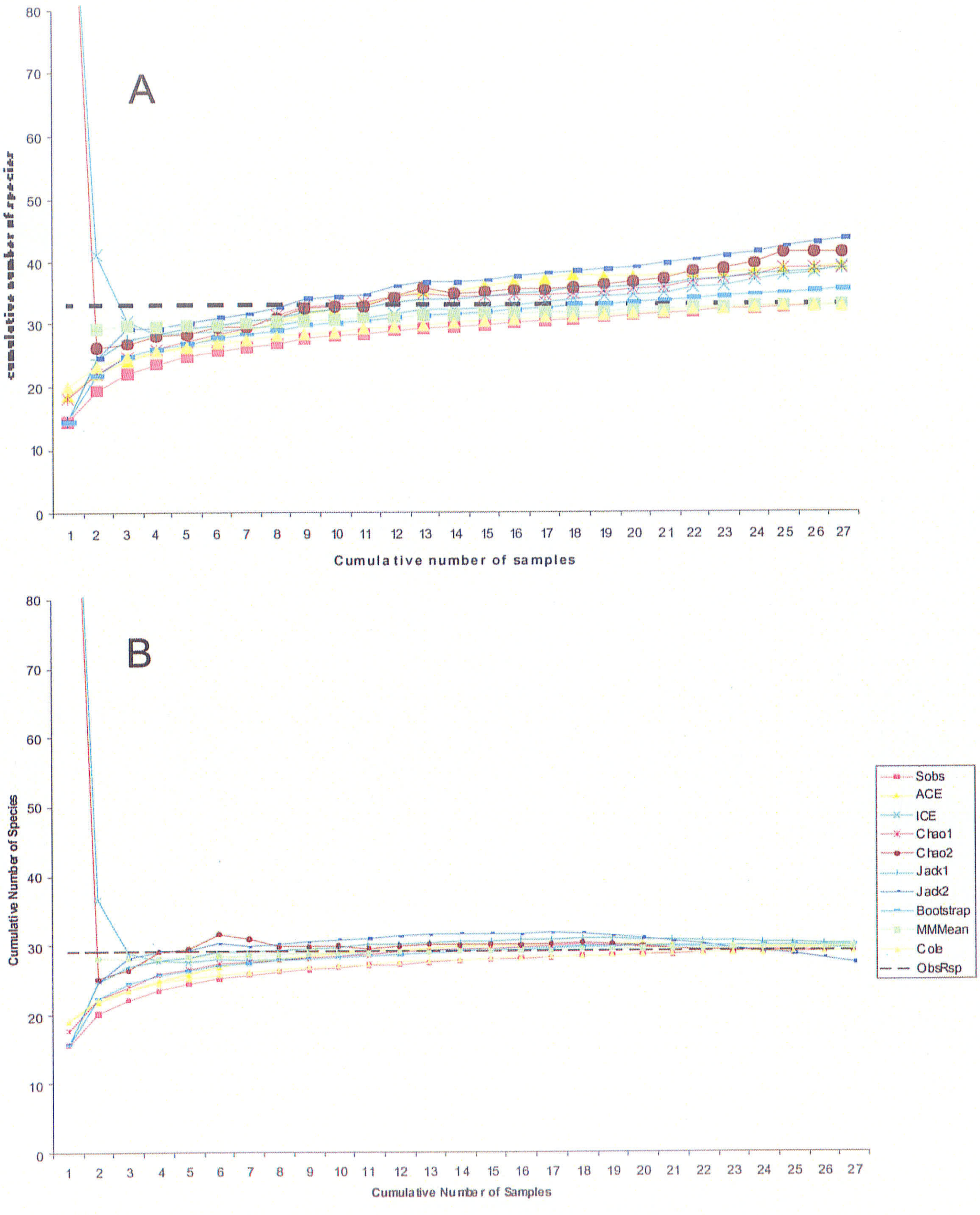

Figure 7.3. Randomized species accumulation curves for the rock dwelling mbuna at (a) Site 8 and (b) Site 13, Thumbi Island West. Note the sample number is 27. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

Richness estimates with a positive bias have a higher proportion of singletons, doubletons, rare, and unique species (Table 7.2, above). For example, Site 8 was the most speciose and 17% of the species observed were singletons. Similarly, rare and unique species at Site 8 accounted for 31% and 14% of the observations. Richness and rarity at Nakatenga Island is relatively low indicating redundancy among the temporal samples is high. Nakatenga had at most one singleton, representing a maximum of 4% of the species counted. The rare and unique species at the Exposed site were most numerous, but only accounted for 19% and 11% of the species, respectively.

The mbuna species density (i.e. number of species/unit area) was 0.22 m^2 for the mbuna, for the 2 – 10 m aggregate depth range. The density of abundance for the male mbuna was 0.61-0.74 m^2. These data suggest that three SCUBA samples in the 2 – 10 m zone may count 85- 90 % of the species, but could be as low as 75%.

A 2x increase in sampling effort at Thumbi Island produced species accumulation curves with different forms because additional sampling yielded two different outcomes; either an increase in redundancy or diversity. At Site 13, additional sampling did not find any new species, and the number of rare species and singletons decreased. This is evident as a change from an asymptotic and positively biased set of curves at 15 samples to an asymptotic form at 27 samples where accuracy and precision of the suite of curves is high. At Site 8, on the other hand, 4 new species of mbuna were observed with more sampling, and the number of rare and unique species increased. I have not attempted to determine the sample size at which this occurs for site 13. I do not speculate at length on the reasons why richness and levels of effort vary by island and site. It is noteworthy that the shoreline of Nakatenga Island is smaller (1370 m) and hosts just of 28 species. In comparison, Thumbi Island West is nearly 4.6x larger (6330 m) and has a total of 44 sp. This may suggest the size of the resource pool from which I sampled at Thumbi West was larger, and was more difficult to exhaust but site characteristics may also contribute to differences in site richness.

7.3.3 *Sandy Shore Haplochromines*

The form of the species accumulation curves for the pooled sample (i.e. all available data) of haplochromines from the shallow (0 - 5 m) sandy habitats was similar. All five sites show most species accumulation curves are non-asymptotic and positively biased (Figures 7.4 – 7.6). The positive bias of the suite of curves overestimates observed richness, on average, by 24 – 43%. Rare species, i.e. those with an abundance less than 11, accounted for the majority of the richness at each of the 5 sites and ranged from 65 to 82% of the observed species (Table 7.3). Of these, the singletons are rampant; they represent from 20 - 40% of the observed species at each site. It is clear in Table 7.3 that rarity, in all of the measured forms, is an inherent characteristic of these samples. Variation in richness and unique species is present amongst sites. The pooled sample was most complete and suggests richness varies along the coast. The maximum species density of the pooled sandy shore samples was at Kambiri (0.007 species/m^2) and Senga Bay (0.006 m^2). All other sites were between 0.002-0.004 species m^2.

Active methods of catching, including seine net hauls, result in the collection of mature and immature individuals of both sexes, and this provides a first opportunity to explore any effect of data partitioning on the form of the species accumulation curve.

Enumeration of mature males accounts for 60% to 85% of the total species observed. As expected, counting all mature individuals results in not less than 91% of the total species observed, suggesting little is gained by the relatively difficult enumeration of immature fishes. All trials in Table 7.3 provided non-asymptotic curves similar in form to the pooled sample. Differences between trials at a site also show that estimated richness varies due to sample size, which in this case is attributed to partitioning by sex and maturity.

As shown in Figure 7.6 (inset F), the modeled species accumulation of the 5 sites approximately maintains the rank order of the observed richness of the sites, and the curves form two main groups. Senga Bay and Kambiri are adjacent and form one group with all others forming the second group. According to the first order Jacknife model and these data, the richness at Kambiri would be expected to achieve a higher richness than at Senga. Indeed, Table 7.3 shows that all measures of rarity at Kambiri are greater than at Senga, except for richness.

The strongest positive bias in these samples was provided by ICE, Chao2, and Jack2. Surprisingly, Chao2 provided an asymptote for the Nkama data. The ICE and Chao1 models demonstrated instability of the initial slope of the curves at low randomized sample number.

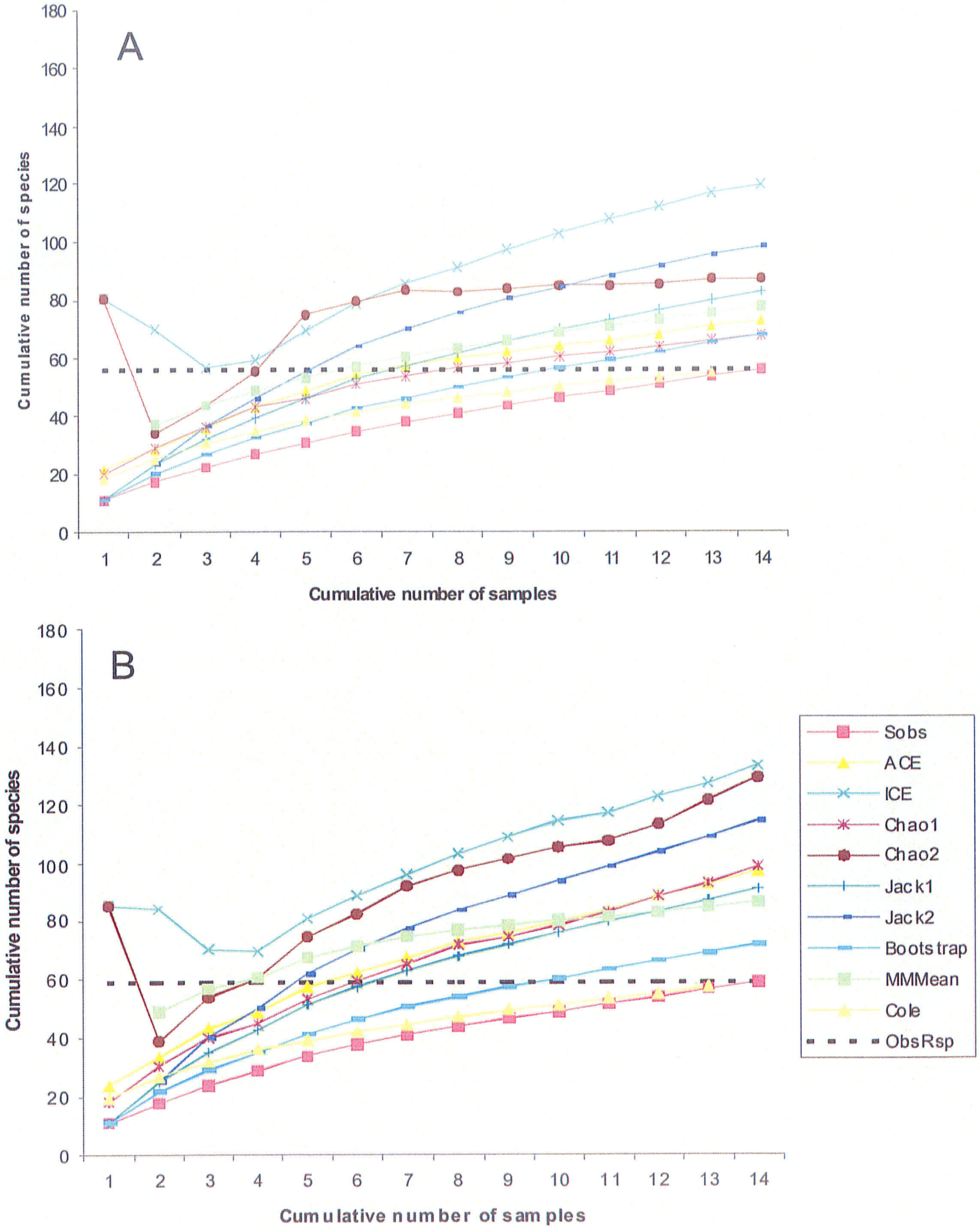

Figure 7.4. Randomized species accumulation curves for the shallow sand shore samples (0-5 m) at (a) Nkama and (b) Nsala. The observed species richness (ObsRsp) is shown using horizontal dashed line.

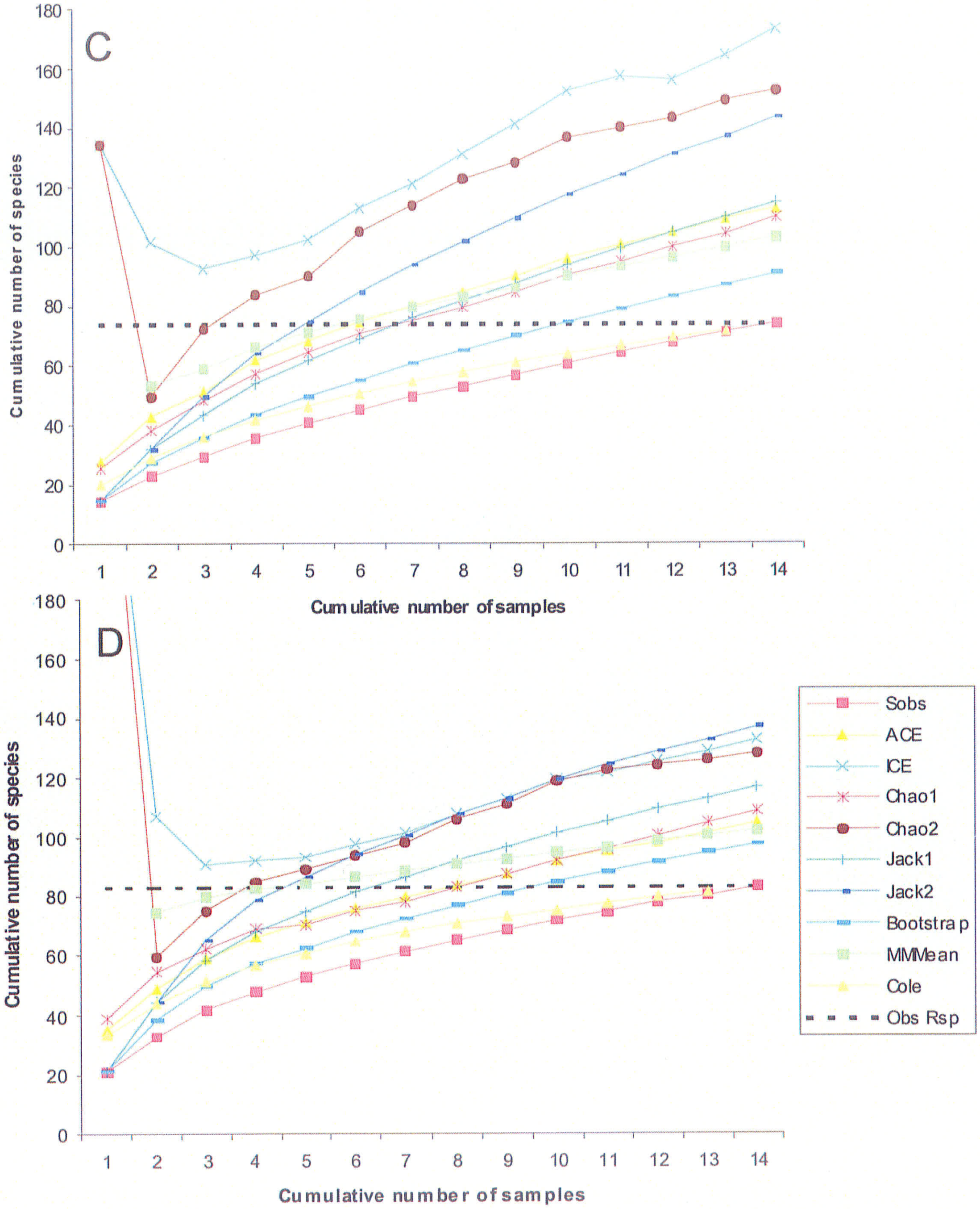

Figure 7.5. Randomized species accumulation curves for the shallow sand shore samples (0-5 m) at (c) Kambiri and (d) Senga Bay. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

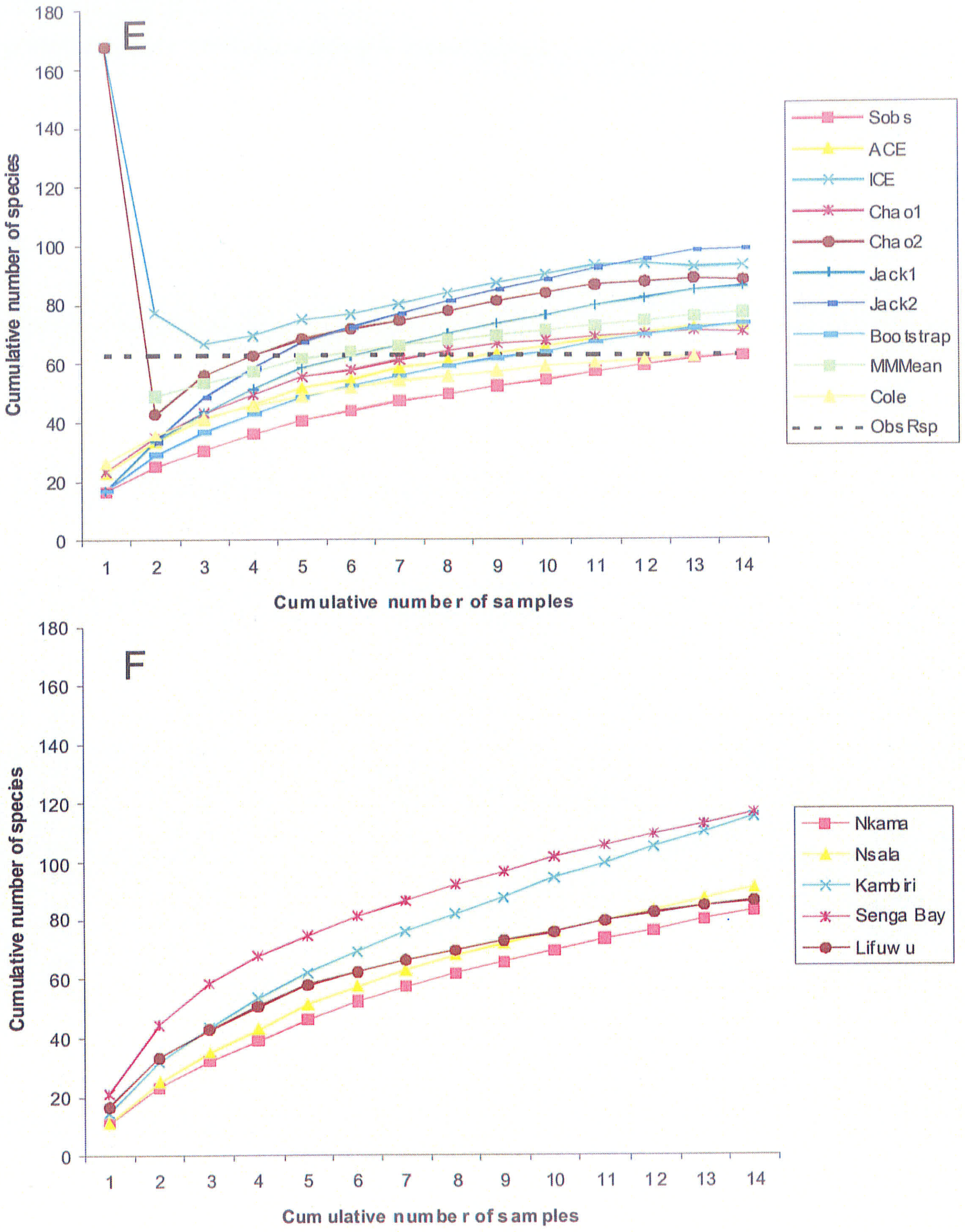

Figure 7.6. Randomized species accumulation curves for the shallow sand shore samples (0-5 m) at (e) Lifuwu. For comparison, (f) shows all 5 species accumulation curves by using the first order jackknife model, chosen at random. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

Table 7.3. Estimates of species richness and summary statistics for male, female, and the pooled sample of haplochromine fishes from 5 sandy littoral sites on the west shore of the southern basin of Lake Malawi. All statistics are derived from 14 seine hauls at each location.

	Nkama			Nsala			Kambiri			Senga Bay			Lifuwu		
	Males	Mature	Pooled	Males	Mature	Pooled	Males	Mature	Pooled	Males	Mature	Pooled	Males	Mature	Pooled
Richness Estimate															
ACE	45.4	64.6	72.9	69.8	91.8	96.9	75.4	104.0	112.7	87.0	91.7	104.7	60.7	74.9	72.5
ICE	66.4	105.7	119.4	113.8	129.9	133.4	86.6	168.1	173.1	98.7	118.0	132.6	105.5	98.6	93.1
Chao1	39.1	58.6	67.4	64.0	99.5	98.7	63.3	101.3	109.9	92.2	91.0	108.4	58.0	74.5	70.4
Chao2	47.7	80.7	87.3	100.9	123.3	129.4	74.8	141.9	153.0	104.2	112.5	128.1	86.0	95.0	88.1
Jack1	49.8	75.1	82.9	67.1	87.6	90.6	66.7	109.0	114.9	88.0	106.7	116.4	79.3	88.1	86.2
Jack2	57.2	89.5	98.3	86.3	110.4	114.2	81.3	136.3	143.9	105.7	123.9	137.0	94.8	103.3	98.9
Bootstrap	41.1	61.5	67.8	52.3	69.7	72.1	53.7	86.3	91.1	73.1	90.1	97.5	65.0	74.0	73.4
MM mean	45.6	67.6	77.7	70.0	85.4	86.3	59.2	102.6	103.1	79.1	95.2	102.0	73.0	78.9	77.1
Observed Richness	34	51	56	42	57	59	44	70	74	62	77	83	54	63	63
No. of individuals	889	2713	2805	870	2676	2727	1056	2221	2286	1925	4655	4768	1148	2792	2880
No. of singletons	11	14	17	18	23	24	18	29	31	21	18	23	11	14	12
No. of doubletons	10	11	11	6	5	6	7	12	12	6	10	9	13	7	8
No. of rare sp.(<11)	26	40	45	34	44	45	35	57	61	45	52	58	43	43	41
No. of uniques	4	7	7	7	7	7	12	15	15	8	9	9	4	5	5

7.3.4 *Offshore Haplochromines*

The form of the species accumulation curves for the pooled samples from the offshore trawls (10 –125 m) generally was similar (Figures 7.7 - 7.10), contained a positive bias, and shows clearly that species richness decreases with increasing water depth, as is evident in the observed data (Table 7.4). For the samples ≤ 50 m where richness and rarity was relatively high, the suite of models overestimated observed richness by 17 – 22%. Rare species in this zone accounted for 28% (10 m) to 18% (50 m) of the total species observed. Below 50 m, abundance is markedly lower and the reduced number of rare species appears to be largely responsible for lower observed richness. Rare species in deep water accounted for 11% of the total species observed. Not surprisingly, the average positive bias of the modeled richness from the suite of curves decreased from 15%, 13%, and 9% at 75, 100, and 125 m water depth. This is corroborated by Figure 7.10, where two groups can be discerned; one group from relatively shallow water (1 – 50 m) over a sandy bottom where initial slopes and richness is relatively high, and another deeper group found over mud, where the same attributes are lower. The species density of the pooled samples diminished with depth from 0.01 m^2 at 10 m, but at greater depths was similar to the sandy shore values (0.006-0.009 species/ m^2).

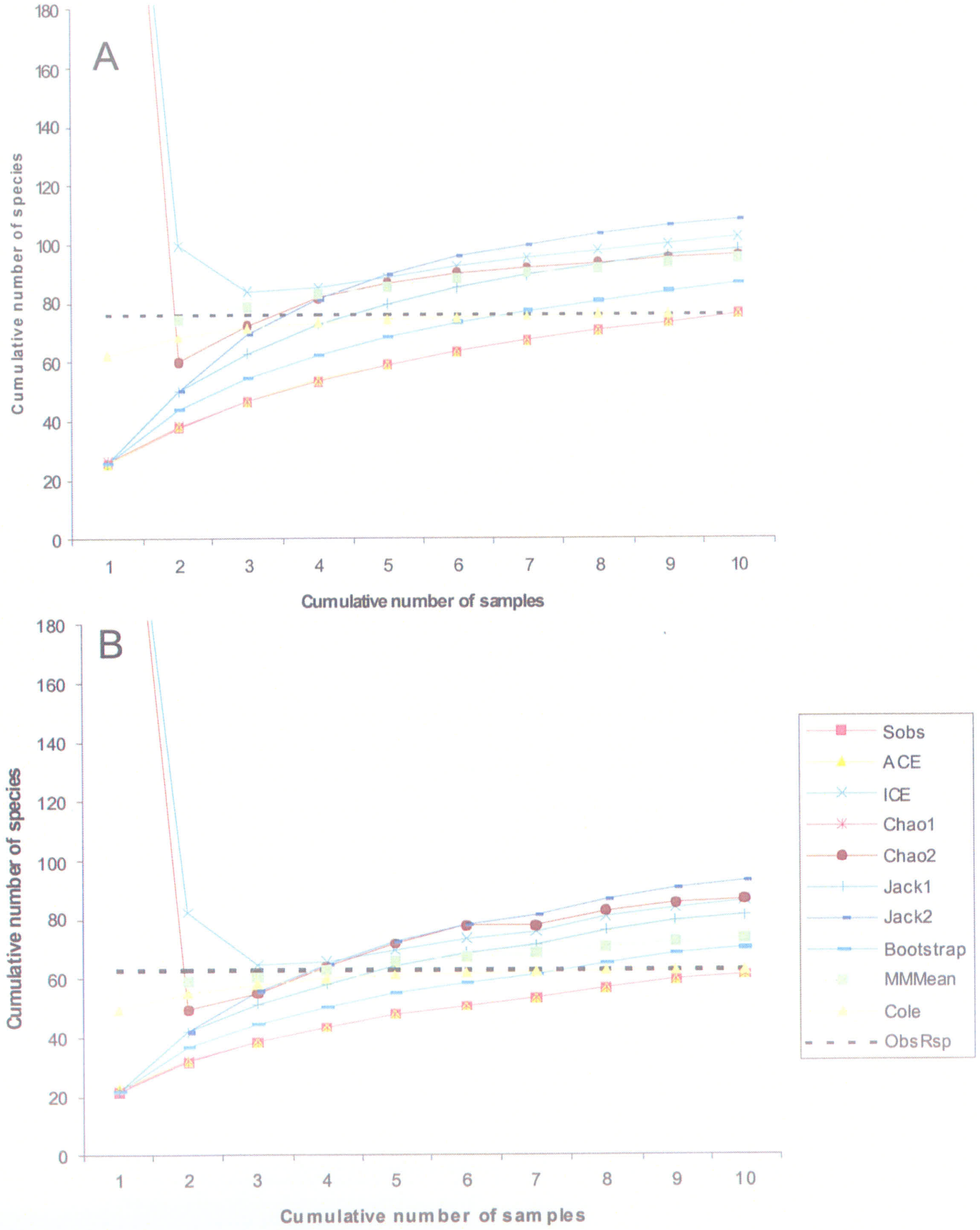

Figure 7.7. Randomized species accumulation curves for the offshore Haplochromine fish at (a) 10 m depth and (b) 30 m depth. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

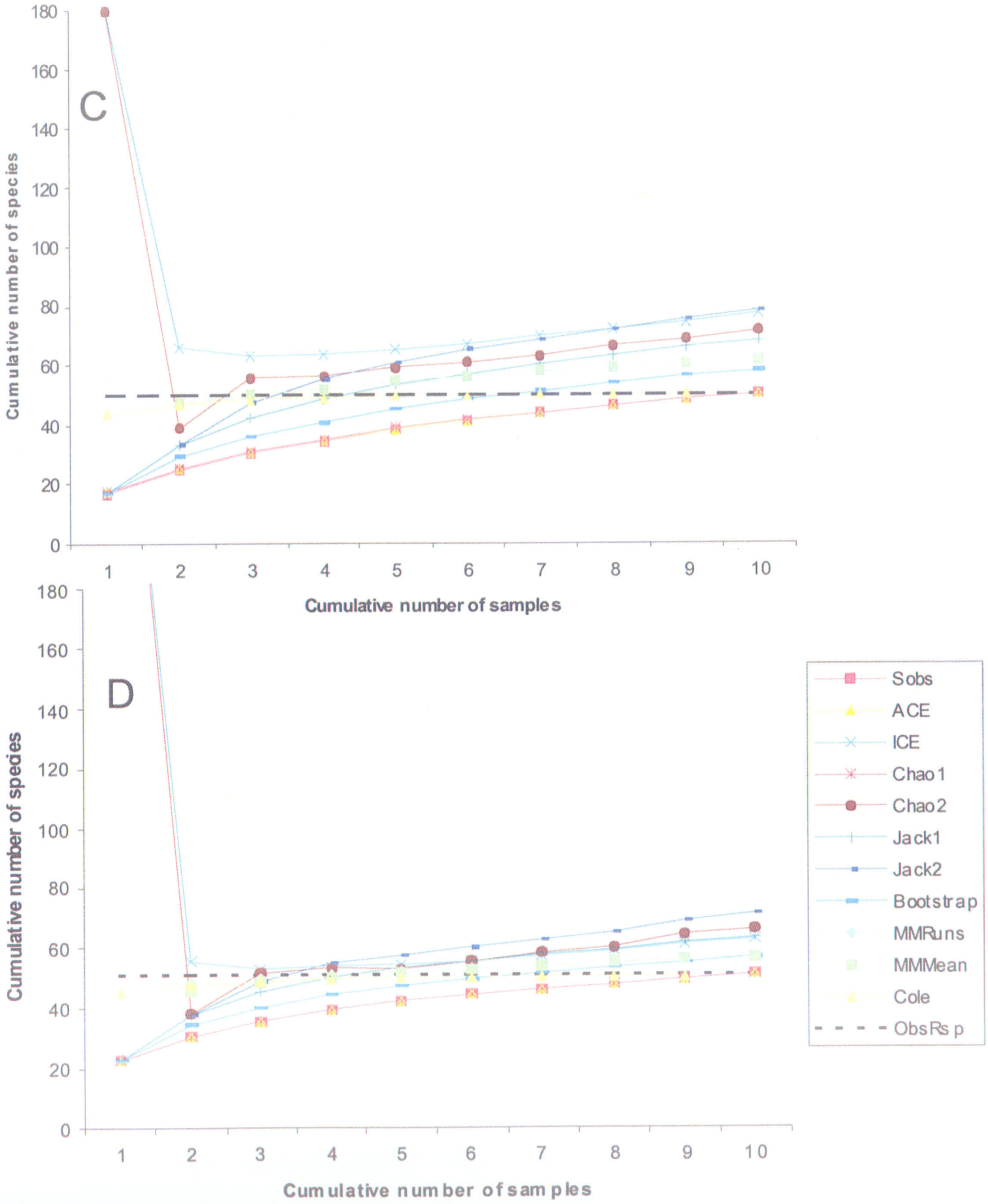

Figure 7.8. Randomized species accumulation curves for the offshore Haplochromine fish at (c) 50 m depth and (d) 75 m depth. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

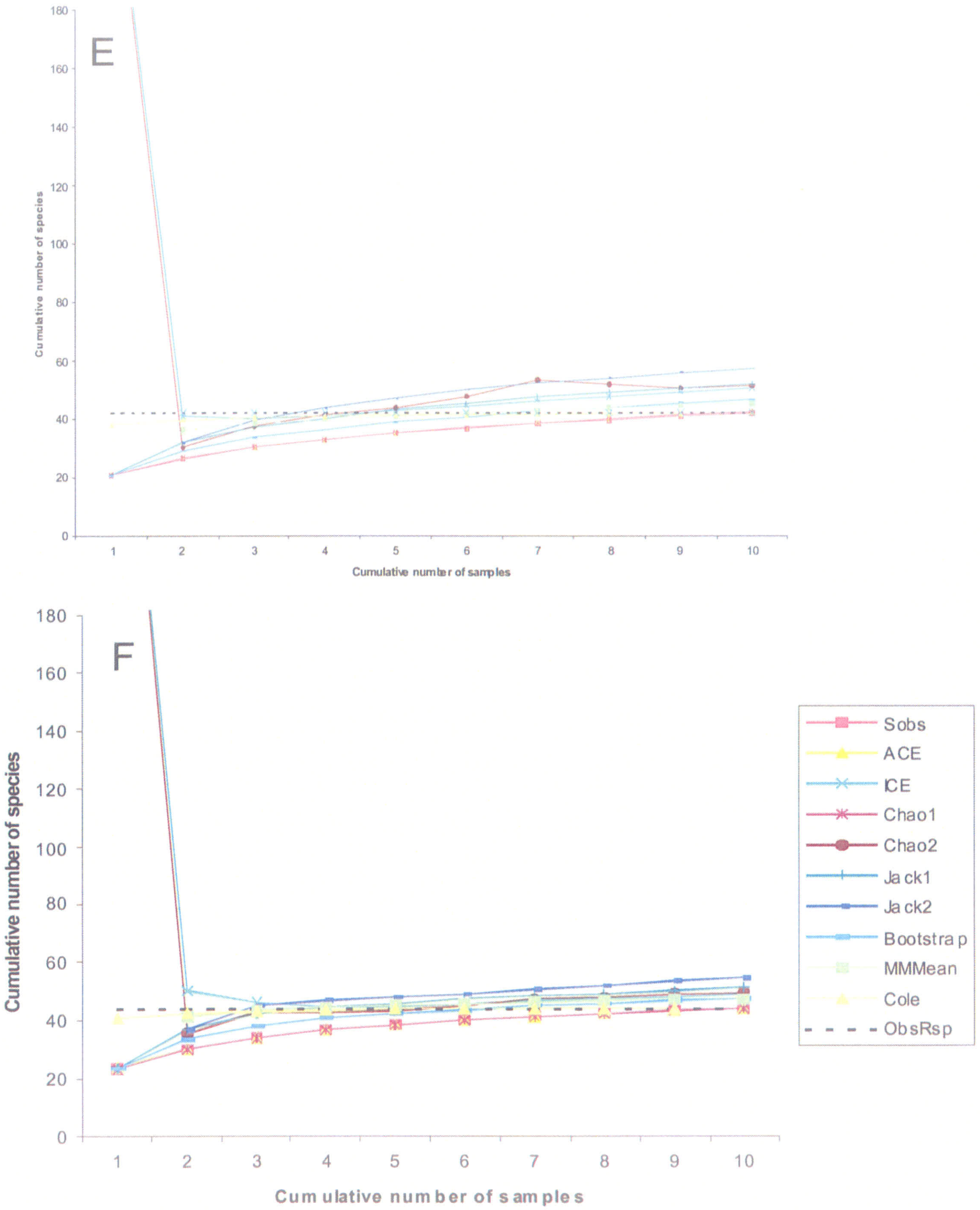

Figure 7.9. Randomized species accumulation curves for the offshore Haplochromines at (e) 100 m depth and (f) 125 m depth. The observed species richness (ObsRsp) is shown using a horizontal dashed line.

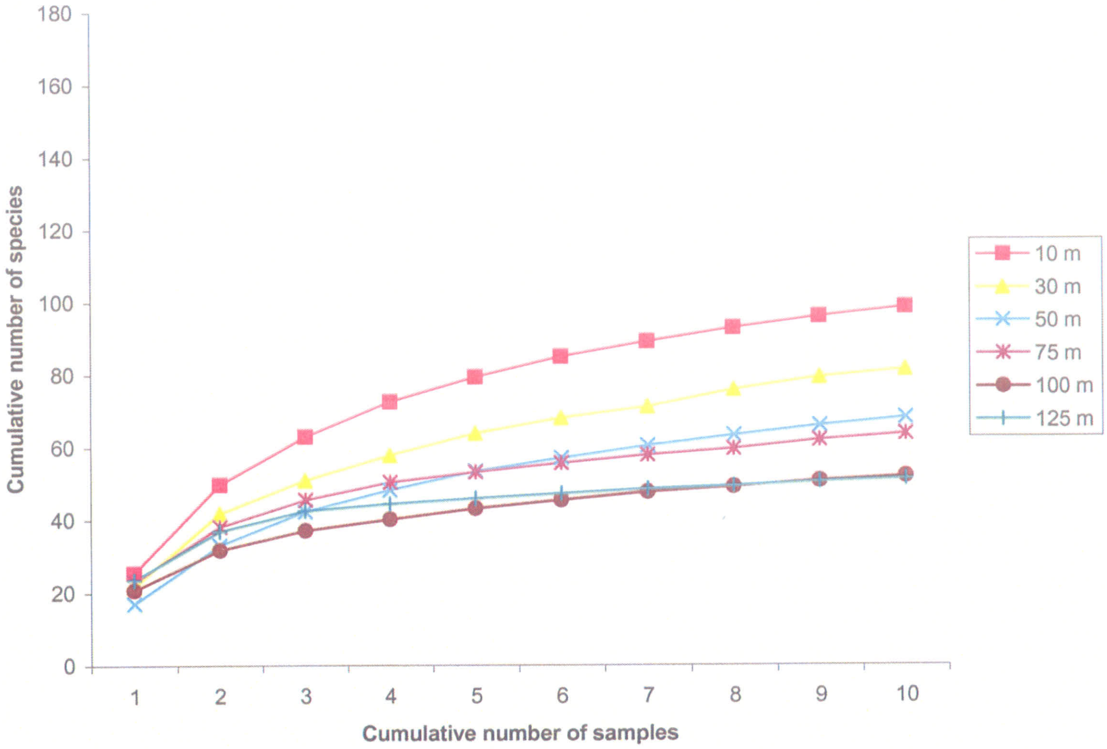

Figure 7.10. Randomized species accumulation curves for the offshore Haplochromines at (a) 10 m, (b) 30 m (c) 50 m, (d) 75 m, (e) 100 m depth and (f) 125 m depth modeled using a first order Jacknife model, chosen at random.

Table 7.4. Estimates of species richness and summary statistics for the pooled sample of haplochromine fishes from 6 depth strata in the southern basin of Lake Malawi. All statistics are derived from 10 bottom trawls at each location.

	10 m	30 m	50 m	75 m	100 m	125 m
Richness Estimate						
ACE	76.0	63.0	50.0	51.0	42.4	44.0
ICE	102.3	89.0	76.8	62.7	50.4	48.8
Chao1	76.0	63.0	50.0	51.0	42.5	44.0
Chao2	96.1	88.4	71.2	66.4	51.3	49.8
Jack1	98.5	83.9	68.0	63.6	51.9	51.2
Jack2	108.5	96.1	78.3	71.2	57.1	54.8
Bootstrap	86.5	72.3	58.0	56.6	46.5	47.4
MM mean	94.9	74.6	61.6	56.8	45.3	47.6
Observed Richness	76	63	50	51	42	44
No. of individuals	90158	90580	105042	75902	48063	44312
No. of singletons	0	0	0	0	1	0
No. of doubletons	3	4	0	3	0	0
No. of rare sp.(<11)	21	18	9	6	5	5
No. of uniques	0	0	0	0	0	0

The Chao1 and ACE models of accrual resulted in complete agreement with observed richness for each depth strata, but unlike all other models ACE formed an asymptote and initiated accumulation at a relatively high richness. ICE and Chao2 demonstrated instability of the initial slope of the curves at low randomized sample number. The second order Jacknife model consistently provided the largest positive bias across all depths.

7.3.2 *Temporal Variation*

The magnitude of variation in abundance over time is higher in the pooled sample than in the abundant species for all three sample groups (Table 7.5). The pooled mbuna (i.e. rare and abundant) demonstrate the lowest magnitude of variation in abundance. The coefficient of variation (V) for the pooled sandy shore and offshore species is 1.7 – 2.0 x higher than the mbuna. Comparison of the abundant species across sampling groups shows that the V of the sandy shore and offshore species slightly greater, 1.9 – 2.6 x the average of the mbuna. The abundant deep water (> 75 m) haplochromines exhibited the lowest magnitude in variation of the fishes inhabiting smooth bottomed habitats (i.e. sand and mud).

The measures of central tendency shown in Table 7.5 describe the frequency of occurrence (i.e. presence/absence of species summed over all sampling events). The pooled mbuna transect frequencies are markedly higher than those of the fishes of smooth bottomed habitats, revealing that most mbuna are encountered frequently during the temporal sampling. In contrast, the likelihood of observing the same sandy shore or offshore species in consecutive monthly samples is markedly lower. For example, sandy shore and offshore species were present, on average (f_{mean}), in 23% - 32% of the transects. In contrast, the average number of transects an mbuna species was observed was frequently greater than 70%. Similarly, the modal number of transects in which a species was observed for the smooth bottomed samples was low (i.e. typically 7 – 17%), but was 100% for the mbuna, indicating many of the species were represented in all samples. The frequency statistics among groups are more similar for the abundant species, but the lower frequency of occurrence of the sandy and offshore species suggests even the list of abundant species will vary over time.

Table 7.5. Average measures of central tendency and relative dispersion for the samples from rocky shores, sand shores, and offshore haplochromines. Values have been standardized across groups by selecting a common time period (December - May) and sampling interval (1 sample/month); n = 6 for each sample group, except for Nakatenga Exposed where n = 5 from October - May. The average frequency (f) data are %. The coefficient of variation (V) was derived from species relative abundance.

Haplochromine			Pooled						Abundant					
Sample	Site	Depth	n	Abundance	f_{mean}	f_{median}	f_{mode}	V	n	Abundance	f_{mean}	f_{median}	f_{mode}	V
Mbuna	8	2	25	790	64	88	100	0.70	11	683	79	89	100	0.48
		6	19	510	68	77	100	0.81	10	455	96	100	100	0.45
		10	17	420	33	11	11	0.97	7	353	58	56	56	0.35
	13	2	21	906	73	91	100	0.43	8	745	88	100	100	0.37
		6	19	684	71	91	100	0.66	8	585	97	100	100	0.29
		10	17	428	66	91	100	1.05	6	306	75	91	100	0.72
	Exposed	2	22	527	78	100	100	0.88	6	302	78	90	100	0.80
		6	22	489	73	80	100	0.89	6	359	73	100	100	0.44
		10	16	415	73	80	80	0.98	4	312	73	90	100	0.75
	Sheltered	2	21	482	71	71	100	0.84	6	336	75	86	100	0.55
		6	19	437	61	57	57	1.09	5	282	79	100	100	0.88
		10	12		71	71	71	0.90	4	205	90	86	100	0.77
	Mean				**67**	**76**	**85**	**0.85**			**80**	**91**	**96**	**0.57**
Sandy Shore	Lifuwu	0 - 5	40	1471	26	14	7	1.87	5	1204	84	89	93	0.79
	Senga Bay	0 - 5	61	2232	25	14	7	1.80	8	1901	76	79	100	1.06
	Kambiri	0 - 5	39	1080	18	7	7	2.06	3	968	95	93	93	1.13
	Nkama	0 - 5	27	1284	21	7	7	1.28	5	1180	73	79	71	1.56
	Nsala	0 - 5	36	950	26	14	14	1.66	6	803	84	82	86	1.09
	Mean				**23**	**11**	**9**	**1.73**			**82**	**84**	**89**	**1.12**
Offshore	Unique Shallow	10	38	34018	33	20	10	1.61	23	33825	56	50	17	1.57
		30	24	34240	31	20	10	1.51	19	34193	52	50	17	1.53
		50	10	15385	33	30	10	1.34	7	15325	74	83	100	1.25
					32	**23**	**10**	**1.49**			**61**	**61**	**44**	**1.45**
	Unique Deep	75	12	10534	38	30	10	1.59	10	10515	58	50	100	1.16
		100	11	10174	56	60	10	1.42	9	10152	81	100	100	1.13
		125	13	12764	44	30	10	1.48	9	12711	70	83	100	1.34
	Mean				**46**	**40**	**10**	**1.50**			**70**	**78**	**100**	**1.31**

7.4 Conclusions

The main focus of this chapter has been to examine the relative levels of species richness across the rock, sand, and mud habitats, and to study the temporal increment in richness and numerical variation of the samples. I designed four questions to provide the basis of the examination: 1) how many sampling events are required to sample sufficiently each of these assemblages?, 2) can one model of species accumulation be applied equally well on all groups?, 3) Does the frequency of presence and abundance vary in the groups or is unchanging?, 4) can the species richness of rock, sand, and mud habitats be reduced to ordinal classes to infer the ranking of areas for conservation priorities?

Research questions 1 and 2 were addressed in the section " The form of the species accumulation curve". Results demonstrated that the non-mbuna and mbuna of rock shores exhibit asymptotic curves of species accumulation suggesting sampling, at different levels of effort, was sufficiently complete. Mbuna and non-mbuna richness varied by study site. A trend was suggested for the mbuna where the smaller island with a smaller species pool required less sampling to achieve an asymptote. This study was the first to document male mbuna and non-mbuna in concert. As many as 59 species were recorded with a maximum species density (i.e. number of species/unit area) was 0.39 m^2, or 0.22 m^2 for the mbuna, for the 2 – 10 m aggregate depth range. The density of abundance for the male mbuna was 0.61-0.74 m^2. These data suggest that three SCUBA samples in the 2 – 10 m zone may count 85- 90 % of the species, but could be as low as 75%.

The majority of sandy shore and offshore samples showed no sign of an asymptote, despite relatively long temporal sampling and very large sample sizes. This suggests rarity is relatively high, the size of the species pool was probably larger than the area sampled, and that sampling was incomplete. This pre-empts question 4. However, the sample of mature adults from the sandy shore data was most complete, and showed richness varied along the coast. The maximum species density was 0.007 m^2. The offshore samples richness decreased with an increase of water depth, as did rarity. Accordingly, species density diminished with depth from 0.01 m^2 at 10 m, but at greater depths was similar to the sandy shore values. The density of abundance for the pooled offshore samples, considered to be virgin stocks by Duponchelle et al. (2003) was highest over sand (i.e. 1.6 - 1.3 individuals/m^2) in water $\leq$ 50. In deeper water over mud the abundance per unit area was lower (1.1 – 0.66 individuals/m^2).

The relative accuracy and precision of the estimators varied across assemblages, and the magnitude of estimated richness depended on the structure of the assemblage and the model. Three of the four mbuna sites studied each provided a suite curves that were both accurate (estimated richness = observed richness), and precise (the estimated value was repeated frequently along the asymptote). In the case of the mbuna, flexibility in choice of model is granted. Site 8 at Thumbi Island West is the exception. Site 8 is believed to be the richest site on the island, and this island is among the richest on the lake. It probably represents a worst case scenario for sampling effort on islands. In general, across all samples, Jack2, ICE, and Chao2 demonstrated the highest positive bias when a positive bias in the suite of curves was evident. ACE, MMMeans, and Chao1 appear to be conservative as a strong tendency to plateau early is shown, and richness at low randomized sample number is overestimated. The ICE and Chao1 models showed instability of the initial slope at low randomized sample number. These models are not good choices if the initial slope is intended for use as a diversity index.

Research question 3 was addressed in the section "Temporal Variation". It was concluded that temporal variation in abundance and frequency of presence relates strongly to rarity but is not limited to it. Temporal variation is lowest in the mbuna assemblages and supports the widely held view that stenotopy of the mbuna is high. The sandy shore and offshore haplochromine cichlids appear to have a shifting and highly variable abundance that ranges from 1.7 – 2.6 x higher than the mbuna. Much of this variation results due to rarity that is confined mostly to the upper 30 m of sandy habitat. Another interesting and novel insight into the deep water assemblage is that rarity and richness is relatively low, and yet temporal variability in the presence of species over time occurs. Apparently, even the ubiquitous deep water fishes are mobile and shifting.

7.4.1 Summary

The accrual and temporal variation of haplochromine cichlid fishes of rock, sand, and mud substratum habitats was studied in the southern basin from 0 – 125 m depth to assess if the assemblages could be reduced to three ordinal classes. The mbuna and non-mbuna of rocky shores on islands live in habitats of finite scale and show asymptotic species accumulation curves, suggesting sampling largely exhausted the species pool. The abrupt asymptote and good statistical properties of the suite of mbuna curves at 3 sites supports assessment of richness according to sampling effort, and reveals richness varies among sites within continuous rocky littoral. At these sites, all but one model converged on the observed mbuna richness; similar behavior by different models in this case is a strong indicator of high redundancy (low rarity).

The assemblages sampled over expansive sand and mud habitats exhibit non-asymptotic forms of accrual with widely divergent statistical properties, and suggests sampling is incomplete. This is despite the fact these samples constitute by far the largest research samples taken from the lake, and counted far more individuals than the mbuna. Some patterns were evident among models with respect to systematic positive bias but a single model cannot be easily chosen for smooth bottomed habitats.

The notion of site richness is a cornerstone in many conservation efforts. It applies well to the rocky shore species because mbuna are a relatively immobile assemblage that can be described well with reasonable effort, and any observed pattern can be expected to persist over time (at least 0.5 yr). In contrast, site richness and abundance over sand and mud habitats varies widely in space and time meaning this assemblage literally is a variable and moving target for conservation.

The present data provide a combination of asymptotic and non-asymptotic curves that prevents an unambiguous ranking of species richness across the rock, sand, and mud habitats. Even if sampling was considered complete across all groups an inequitable comparison would result because counting mature males on the rock shores is a negatively biased index when compared to the pooled samples from the smooth bottomed habitats. This reveals a major deficiency in understanding of the ecology of the difficult to identify female mbuna. The ordinal ranking of richness across the major habitats is further complicated by differences in passive and active methods of data collection.

The benefit of hindsight suggests the approach of advocating a single model to rank richness across the three main habitats is not particularly useful. First, as noted above, the complete form of all the curves has not yet been derived and prevents any ranking. It is important to note that these data are, however, the first from a single study that show clearly a large gradient of richness and rarity and that the shape of the curves reflects these attributes. At this early stage, therefore, I have found more utility in using the full suite of models as a diagnostic measure (i.e. graphic index) of rarity and sampling completeness, than to use any single model to estimate richness. Secondly, this chapter has shown clearly that the differences in the frequency of presence, changes in abundance, and preliminary estimates of density between the rock, sand, and mud (i.e. Deep water) fishes are marked. Further, a synthesis of the main results of this dissertation suggests the conservation units will be: 1) markedly different in size (Chapter 6), 2) stratified by deep water and shallow water (perhaps by the mud boundary) (Chapter 5), and 3) in largely an alternating pattern around the basin (Chapter 4). Based on this novel information it seems most appropriate the haplochromine species inhabiting the rock, sand, and mud (i.e. deep water) habitat zones be considered unique challenges for conservation and management. I conclude that these assemblages are so different that the perspective of relative importance implied by ordinal ranking be dropped.

Chapter 8 Conclusions, Summary, and Recommendations

8.1 Conclusions

This chapter provides: 1) an overview of the main goals of this dissertation, 2) a chapter by chapter summary of results, 3) a summary and concluding remarks, and 4) recommendations that continue towards the aim of developing a conservation and management plan for Lake Malawi based on this new synthesis of information.

8.1.1 Overview of Main Goals:

This dissertation aims to address two main goals: The first is to assess if physical habitat distributions influence the species composition of the haplochromine cichlids and questions the role of persistent versus ephemeral influences on the species. The second main goal is to assess if the species data can infer the relative size of any management units, and if species richness can infer relative importance among the assemblages for priority in conservation.

The first goal is important because it enables the development of conservation strategies that recognize and adopt the geographic framework that has played a part in the evolution of the haplochromine cichlids. This approach is a proxy that attempts to circumvent the need for complete and detailed taxonomic information, and instead use habitat patterns that are readily observed and temporally invariant. Complete biological inventory of the diversity in this lake is a daunting task and in all likelihood is going to take longer than conservation can wait. In this approach I do not advocate that the use of habitat distributions as a spatial template for biodiversity conservation replaces any other approach, but instead forms a first step. It is hoped that the synthesis of physical and biological data is used to better partition the system and focus future studies.

The second goal is important because it attempts to harmonize the management of the species by recognizing the ecology of the assemblages can be used in part to derive a conservation planning scheme, and weigh the relative importance of the main assemblages. The primary emphasis of the biological chapters is to illustrate, for the first time, the main ecological differences of the fishes between the three main habitat types so this information is available to conservation planning.

8.1.2 Chapter Summaries

In Chapter 2, I first described the geomorphologic and tectonic framework of the Malawi Rift, reviewed the processes that form and maintain physical habitat, reviewed technology to acquire coastal and littoral data, and described two mechanisms thought to contribute to the fish diversity. From this it became clear the regional climate, structure of the rift and the expression of mass wasting sets the availability and scale of physical habitat, and that the forcing processes appear to be structured hierarchically with feedbacks that occur across all spatial and temporal scales. Merit for use of remote sensing was demonstrated. It became evident that a combination of allopatric (i.e. extrinsic) and sympatric (intrinsic) speciation probably has contributed to divergence. A lack of information for the fishes inhabiting sand was conspicuously absent.

In Chapter 3, I opted to test the ability of satellite-based synthetic aperture radar to discriminate the coastal zone due to the need for habitat distributions, the large size of the lake, and persistence of cloud cover. Three research objectives were designed to provide evidence to assess this potential: 1) investigate the effects of system parameters, i.e. incident angle and look direction, on SAR backscatter for each class, 2) Assess if SAR backscatter and topographic variables can discriminate and classify rock, sand, and vegetated coasts, and 3) Assess the merit of combining SAR + optical data to evaluate an entirely remote approach to discrimination and classification.

Results supporting objective one showed that look direction and incident angle effects on sigma naught are generally small, and the average backscatter from rock, sand, and vegetated coasts is statistically similar. While the effects of coastal geometry and diurnal changes in moisture availability appear to influence the magnitude of the backscatter, preliminary evidence showed that marked differences only resulted due to a combination of ideal sensor to target geometry in concert with recent rain. SAR sensing of rock coasts must ensure the look direction faces towards the coast to avoid radar shadow. A limitation of the study was that most of the rock coasts in this study provide good sensor to target geometry. Objectives 2 and 3 conclude that classification of the data is excellent. The failing of the method is mainly technical and requires improved remote ability to georeference the SAR images. The results demonstrate clearly the effort applied towards this novel application was merited.

In Chapter 4, three main themes illustrated the need to 1) understand habitat distributions at the lake-wide scale and how the landscape influences the distribution and scale of habitat, 2) to study first-hand the features of a highly controversial low lake stand, and 3) to show the influence of the regional habitat distributions on the mbuna. In theme one, the habitat framework of the lake was acquired using aerial frame surveys, and showed clearly that rift scarps have mainly rock coasts of high slope, whereas depositional areas of the lakeshore plains are mostly vegetated and low slope. Erosional coastlines are juxtaposed between these two in the topographic sequence, have a moderate slope, complex shoreline configuration, a higher number of classes, and most of the mixed classes. The length of rock, sand, and vegetated coasts each are significantly different when compared by landform, indicating the major and minor constituents of the coast can be inferred by the geomorphologic setting. It was concluded that the coastal geomorphology is a strong indicator of the predominant material types and also sets the scale and continuity of coastal habitat. Results supporting the second theme confirmed the attributes that lead Owen et al. (1990) to claim a low lake stand on the east shore of Domwe Island were still present. The interpretation of historic processes using contemporary substratum patterns is, however, uncertain. The gravel deposit claimed to be a paleoshore was confirmed, but this study also illustrated the fact that gravel is strongly associated with rift scarps, like Domwe Island. The literature implies water movements in this area extend to the lakebed, which explains the sediment free deposit at great depth, but the origin of the gravel feature remains uncertain. The last theme of study showed information the pattern of regional mbuna composition (Snoeks, in press), bears a strong resemblance to the to the distribution of coastal habitat. Interestingly, this pattern did not show evidence of recent desiccation, and so appears to support the growing consensus in the research community that low lake stands are older than suggested by Owen et. al (1990). When the correspondence between the coastal habitat and landform type is considered, it was concluded that the tectonic framework of the basin imparts a strong influence on the regional distribution of rock dwelling mbuna.

In Chapter 5, I continued to examine the theme of habitat discontinuities from Chapter 4, but shifted from the coastal zone to the littoral to assess habitat boundaries in deep water. The sand/mud boundary marks the upper limit to the profundal zone of perennial deposition and was observed at all study sites, usually between 65 – 100 m depth. The importance of this deep water habitat discontinuity is threefold: 1) the position of the boundary is an environmental indicator that reveals the abrupt transition from the erosive and coarse grained shallows to the depositional and fine grained offshore zone, i.e. the littoral and profundal, 2) the mud boundary completes the habitat template in this study by providing an offshore boundary that compartmentalizes the alternating segmentation shown in Chapter 4, and 3) because sedimentation is a concern for the lake but is an ephemeral process, methods for mapping the mud boundary enabled comparison of sites in steady state (unaffected by sediment) to another out of steady state (effected). This result highlighted the point that the mud boundary is much more shallow (about 30 m) in an area adjacent to a major river delta than at all other study sites away from sources of sediment. The superimposition of sediment on sand and sand/gravel was observed and suggested the littoral zone is likely smaller than in the past.

Most of Chapter 5 documented the development of a remotely based approach for bottom typing and demonstrated the strengths and limitations of the classification. Multivariate analyses showed the relationship between the 2 acoustic and 1 topographic (i.e. slope) variables was highly significant. It is not a surprise that only two acoustic variables performed well because hardness and roughness are largely uncorrelated (each provides new information), and this property is known by the developer of the hardware. The acoustic response of the validation data illustrate two interesting and novel points: 1) the magnitude of the acoustic response from a rock substratum is highly variable, 2) the magnitude of the acoustic response from largely planar bottoms decreases markedly at high angle of incidence (i.e. ≥ 30 degrees), mimicking a response expected from a mud bottom where the acoustic pulse largely transmits through the sediment volume and is absorbed. The multivariate discrimination and classification results illustrate that this is the main source of error in classification. It was surprising to find that this source of error resulted in misclassification between rock and sand (i.e. not rock and gravel). Apparently, the losses due to oblique scattering on rock result in signatures more like sand, than the high magnitude (but low roughness and low slope) of gravel deposits in this dataset. It is now evident that that a logical connect exists between Chapters 3 and 5. I conclude that the principal form of confusion when classifying complex rock surfaces using active forms of remote sensing, in this case synthetic aperture radar and sonar, results due to losses from forward scattering.

Results from Chapter 6 provided exciting new insight into the ecology of the haplochromines inhabiting the Lakeshore Plains. The two main research questions involved study to assess: 1) Do habitat discontinuities at local scales influence species composition, and do ephemeral changes in the environment cause seasonal shifts in the composition? 2) What are the relative roles of evolutionary (space, time) and environmental variables (depth, temperature, total suspended solids) that account for variation in the species data?

Results showed clearly that species composition is strongly influenced by temporally invariant habitat discontinuities and that the effect of seasonal variables (i.e. water temperature or TSS) is relatively small. The finding that mbuna species composition changes between rock outcrops supports a wide body of literature that the mbuna are stenotopic and have restricted ranges within the rocky zone. The finding that most of the haplochromines found over mud in deep water are different than those found over sand in the shallows is new, and provides important ecological information that suggests for the first time three largely unique assemblages inhabit the three main substratum habitats in the lake. Also, for the first time we have evidence that rarity is high in the sandy shallows and is largely contained in water less than 30 m. Both of these new results have significant value for conservation planning.

The influence of TSS on species composition is limited but is considered inconclusive. Since my field work, new information is available (G. McCullough pers. com.) that suggests the periodicity of the plume dynamics in the study area and the sampling interval are at a mismatch. Still, the spatial structuring of the mbuna at Nakatenga Island was reduced when compared to Thumbi Island West. Results on this are also considered inconclusive due to differences in the spacing between sites on each island and no other sites in unaffected areas were available for comparison.

The influence of Space and Time on the datasets suggests that the sandy shore and offshore datasets behave similarly and contrast strongly to the mbuna on rock shores. This suggests differences can be reduced to the smooth and rough bottomed habitats. In general, the importance of Space as an explanatory variable for differences in composition for the rough bottomed habitats is high, and the influence of time is very low. In contrast, the effect of Space on the composition of the assemblages of the smooth bottomed habitats was relatively low, despite a sampling frame that spanned nearly twice the distance of the mbuna studies. Accordingly, time was more important for the smooth bottomed assemblages but especially so in the deep water. This appeared to result from high rarity in shallow water but because rarity in deep water is relatively low this provided evidence of a shifting character by the ubiquitous and abundant species. The importance of Space and Time as explanatory variables for differences in composition appear to be inversely related and may provide preliminary evidence of static and mobile assemblages. The present data therefore suggest that the size of rock, sand, and mud (i.e. deep water) conservation areas would probably ordinate as small, medium, and large, respectively. The length of the units along the coast could mirror the rock habitat distributions but the absolute size of any zones on the extensive Lakeshore Plains remains speculative.

Chapter 7, the final research chapter, continued the study of the 3 haplochromine datasets of Chapter 6 but focused on the magnitude of richness and investigated the temporal variation of the samples during the accrual of species. This approach was designed to reveal the relative richness of the three main assemblages (rock, sand, and mud (i.e. deep water)) and to further explore the preliminary findings of Chapter 6 that suggested the fishes on smooth bottomed habitats are mobile.

The richness of the rock, sand, and mud (i.e. deep water) habitats cannot be compared directly due to incomplete sampling of the smooth bottomed habitats, evident as non-asymptotic species accumulation curves. It was concluded that ranking of the richness of the assemblages was ambiguous. Results demonstrated that the haplochromines inhabiting rough bottoms exhibited markedly asymptotic curves of species accumulation that indicated sampling rapidly exhausted the species pool.

The differences evident between the SAC'c for the rough and smooth bottomed habitats was also apparent in the temporal variation statistics. During the temporal sampling, the mbuna had the highest mean frequency of occurrence and lowest variation in abundance. The sandy shore and offshore haplochromines have a shifting species composition and highly variable abundance that ranges from 1.7 – 2.6 x higher than the mbuna. Some of this variation results due to rarity that is confined mostly to the upper 30 m of sandy habitat. Temporal variability in the presence of species over time also occurs in deep water despite lower richness and low rarity; apparently, even the ubiquitous deep water fishes are mobile as represented by a shifting species composition. It was concluded that temporal variation in abundance and frequency of presence relates strongly to rarity on the smooth bottom habitats but is not limited to it. The concept of site richness applies well to the assemblages in rough bottomed habitats, but the haplochromines inhabiting smooth bottoms is literally a moving target for conservation.

8.1.2 Summary and Concluding Remarks

The results of this dissertation provide insight into two main questions that are supported by five chapters of research. These chapters contain new techniques that benefit biodiversity research in general, and develop a synthesis of novel results that span physical geography, biogeography, and ecology. This interdisciplinary study will improve significantly our ability to perceive plans for conservation and fisheries management on Lake Malawi.

Evidence is strong to suggest that physical habitat distributions (substratum distributions and/or depth) can be used to infer changes in haplochromine species composition. The effect of these boundaries on species composition was demonstrated clearly for the mbuna between islands and at regional scales for the entire lake. The mbuna composition appears to mimic the structure of the rock habitats that appears hierarchical (i.e. nested) and results from the regional alternating half graben structure, and locally on the escarpments from the spacing of sandy deltas below incised river valleys. The horizontal and vertical extent of rock will provide an effective delineation of park boundaries for the mbuna. Regional endemism and local habitat distributions are primary considerations for conservation planning for the mbuna.

This research also demonstrated that the haplochromine species that inhabit the sandy shallows (0 – 50 m) are quite different from those that inhabit mud in deep water (> 50 m), and that rarity of the sandy shallows (<30 m) is high. This is the first study that shows the haplochromines can be perceived as three general groups, not two, as previously thought. These have significant repercussion for fisheries management and biodiversity conservation.

The haplochromine species composition suggests the relative size of rock, sand, and mud (i.e. deep water) management units would ordinate as small, moderate, and large. Uncertainty remains in the absolute length and area of the sandy (0 - 50 m) and mud (i.e. deep water) fisheries management zones. Also, it has not yet been demonstrated that the rare and ubiquitous species found in the sandy shallows (<30 m) have ranges that are similar, and so the shallow sandy assemblage is considered an aggregate. This study suggests that parks for the mbuna will be small and reflect habitat distribution at local scales and be distributed around the lake within each half graben. The limited mobility of the mbuna means allocation of any parks will impart a bias for conservation of particular species. Alternatively, the sandy and mud (i.e. deep water) species appear to be a roaming and numerically variable target for management. In areas already inhabited by numerous coastal fishing communities (see Cooley et al. 2003) the size of a management unit could be much smaller than the range of a species. Therefore, a preserve (i.e. an area permanently closed to exploitation) of same size could not exclude extinction of any species. To balance the need for resource use and yet reduce the likelihood of extinction, a series of management zones along the lakeshore may need to alternate season openings and closures over space and time. In underdeveloped areas of the Lakeshore Plains it may be feasible to have zones that are permanently closed (i.e. to fishing and coastal habitation) set within a regional series of management units, and could serve as source for recruitment to the other management zones.

8.2 Recommendations

The results of this research suggest further work is needed to clarify the present results, direct future research, and contribute to the design of an aquatic conservation and management plan for the Haplochromine cichlids. These are provided here and are followed by suggestions to guide efforts by a conservation team.

1. *Develop classification methods that include the sequential variability in the microwave or acoustic signal over space/ time as a source of information.*

The problem of forward scattering discussed in Chapters 3 and 5 requires innovative procedures to minimize this error in the future. The success of the SAR classification method, in part, was due to the use of backscatter averages derived from segments of coast 150 m long because the variability in the data was large. Without averaging the method would have failed. It became clear when reviewing the SAR image and sonar data closely, that the sequential variation of signal from both platforms was frequently quite different between classes. Unfortunately, coastal and littoral applications are largely unexplored and there was no readily available way to extract the sequential variability from the satellite image along the coast because raster processing methods are row sequential (methods are not available that follow the coast). In the case of sonar, sequential signal processing could have been implemented over a small area. However, when the complicating effect of incident angle was uncovered it was deemed a slope calculation would also be needed. Such improvement to the method was not within the present scope.

2. *Replicate temporal sampling of the mbuna to assess spatial structuring*

Further temporal study is merited on islands and the mainland coast to better appreciate the degree of spatial structuring. Given that observation in turbid water is difficult, I recommended more studies be undertaken on islands and on the mainland coasts away of the areas where sediment is known to occur seasonally. These data will help to better understand this question and also provide new and reliable information.

3. *Validate the hypothesis that the mud boundary is the main factor in setting species composition in the lakeshore plains areas of the lake.*

To validate the working hypothesis that the mud boundary is the main factor in setting species composition the sites of Tomasson and Banda (1996) in the SE Arm, Duponchelle and Ribbink (2003) in the SW Arm, and the site at Thumbi Island West (Chapter 5) are suitable because the depth of the sand/mud boundary varies among all three sites. Future sampling designs should take advantage of the fact that the transition from sand to mud frequently is abrupt (Rowan et al. 1992, Chapter 5) enabling systematic sampling both sides of the mud boundary in addition to sampling stratified by depth.

4. *During the continued study of the haplochromines inhabiting smooth bottomed habitats consider critically the dispersal ability of the rare vs. ubiquitous species.*

Rarity is, unfortunately, the statistical equivalent of uncertainty. A study that addresses the question of the ranging ability of the rare haplochromines inhabiting sand cannot be recommended as a primary objective due to large effort and limited return, but as information on the shallow sandy fishes grows this question should be considered. Any such effort may be best placed in the southern basin south of Domira Bay where information on these species is most well known.

5. *Replicate studies in the central and northern regions of the lake to validate the observed response of fish ranges to habitat distributions.*

This includes the study of the mud boundary with the improved sampling design noted in Chapter 5 that helps to better assess the relative importance of the mud boundary vs. depth to determine if the groups are shallow and deep, or sand and mud. The shoaling margins of the Mbamba and Livingstone half grabens are suitable areas for future validation. Given the south east arm of the southern basin appears not to be entirely deposition like the southwest, a study that compares the composition of the deep water haplochromines east of Domwe could provide a useful comparison to the 100 and 125 m trawl sites north of Domwe and may help to illustrate the importance of substratum discontinuities in deep water.

6. *Develop a habitat distribution map for the lake that details approximately the horizontal and vertical extent of rock, sand, and mud (i.e. deep water) habitats.*

Using the proposed substratum information (from point number 3), delineate the 40 m contour for the rock habitats and the mud boundary or a depth contour for the littoral areas found in the lakeshore plains. Using the habitat template, segment the coastal and littoral data and classify the coastal zone data. Most of the central and northern regions of the lake will be bounded by the lower limit of oxygenated water.

7. *Contingent upon results of the above, form a Biodiversity Conservation and Fisheries Management workgroup tasked with development of a prototype conservation and management plan for the lake based, in part from the habitat map of recommendation 6, above.*

8. *Establish a steering committee that sets the guidelines and manages the process undertaken by a team of experts in the fields of conservation/parks planning, taxonomy, and fisheries management from Malawi, Mozambique, and Tanzania.*

Supplementary guidelines are provided below to support the steering committee and initial efforts by the local experts:

- Stratify the zonation of conservation management units within each half graben by rock, sand, and mud (i.e. deep water).
- Consult the digital companion to this dissertation, A Biodiversity Atlas for Lake Malawi, version 3.0 (Cooley et al. 2003) for the current databases including the data presented in this work, and new information including maps of coastal village habitation, fish drying racks, and canoes to assess where population density and fishing pressure are relatively high.

- A specific workgroup should be tasked for the more complicated issue of fisheries management in the south-east arm where fishing and habitation is most concentrated. In such areas the size of management zones may need to be smaller than elsewhere in the lake (to avoid relocating villages due to closed zones), and a pattern of shifting closures may need to be planned.
- Many other sandy areas of the lake are uninhabited and this enables the location of new settlement to be decided in advance and to work in harmony with the conservation and management plan.
- The southwest arm has nearly 60 km of continuously vegetated shores. This shallow and large vegetated region is unique and remains unexplored by science.
- The rock coasts, at least on the border faults, may be considered as metapopulations. This could mean that conservation of this group in fact should support the entire sequence of local populations along a border fault due to apparent interconnectedness. This is far too large a unit to manage reasonably and so a compromise is suggested. Snoeks (in press) recommended for the mbuna that "more smaller" is probably better than "fewer larger" conservation units. I agree but add that several smaller units may be placed as a contiguous group. This could help to conserve biota unique to particular stretches of a border fault (e.g. one group below Usisya and another to the north) and enable lateral movement across habitat patches.

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Appendix A:

Rocky shore mbuna sampled at Thumbi Island West and Nakatenga Island.

Appendix A: Rocky shore mbuna sampled at Thumbi Island West and Nakatenga Island.

Cynotilapia afra
Genyochromis mento
Labeotropheus fuelleborni
Labeotropheus trewavasae
Labidochromis gigas
Labidochromis vellicans
Melanochromis auratus
Melanochromis chipokae
Melanochromis crabro
Melanochromis joanjohnsonae
Melanochromis melanopterus
Melanochromis vermivorous
Petrotilapia genalutea
Petrotilapia mumbo blue
Petrotilapia nigra
Protomelas taeniolatus
Pseudotropheus aggressive blue
Pseudotropheus aggressive brown
Pseudotropheus aurora
Pseudotropheus elongatus brown
Pseudotropheus elongatus slab
Pseudotropheus heteropictus
Pseudotropheus livingstonii
Pseudotropheus tiny
Pseudotropheus tropheops gracilior
Pseudotropheus tropheops intermediate
Pseudotropheus tropheops lilac
Pseudotropheus tropheops orange chest
Pseudotropheus tropheops red cheek
Pseudotropheus zebra
Pseudotropheus zebra callainos
Melanochromis parallelus
Petrotilapia tridentiger
Labidochromis pallidus
Petrotilapia fuscous
Petrotilapia yellow chin
Pseudotropheus aggressive yellow head
Pseudotropheus aggressive zebra
Pseudotropheus barlowi
Pseudotropheus burrower
Pseudotropheus tropheops lilac maleri
Pseudotropheus tropheops maleri blue
Pseudotropheus williamsi
Pseudotropheus zebra black dorsal
Pseudotropheus zebra red dorsal
Pseudotropheus zebra yellow throat

Appendix B:

Haplochromine fishes seined at 5 sandy shore sites (0 - 5 m) on the west shore of the southern basin of Lake Malawi.

Appendix B. Haplochromine fishes sampled at 5 sandy shore sites (0 - 5 m) on the west shore of the southern basin of Lake Malawi. * denotes rare species with abundance <11.

Alticorpus 'geoffreyi'*
Alticorpus mentale*
Aristochromis chrysti*
Astatotilapia calliptera*
Aulonocara 'gold'*
Aulonocara guentheri*
Aulonocara macrochir*
Aulonocara 'minuta'*
Aulonocara 'pink head'*
Aulonocara 'pyramid'*
Aulonocara spp.*
Buccochromis atritaeniatus*
Buccochromis heterotaenia*
Buccochromis lepturus
Buccochromis nototaenia
Buccochromis oculatus*
Buccochromis rhoadesii*
Buccochromis spp.
Caprichromis spp.*
Champsochromis caeruleus*
Champsochromis spilorhynchus*
Chilotilapia rhoadesii*
Copadichromis chrysonotus*
Copadichromis eucinostomus*
Copadichromis pleurostigma*
Copadichromis 'spotted'*
Copadichromis spp.
Copadichromis trimaculatus*
Copadichromis virginalis*
Corematodus taeniatus*
Ctenopharynx intermedius*
Ctenopharynx nitidus
Ctenopharynx spp.*
Ctenophaynx pictus*
Cyrtocara moori*
Dimidiochromis compressiceps
Dimidiochromis dimidiatus
Dimidiochromis kiwinge
Dimidiochromis spp.*
Dimidiochromis strigatus*
Diplotaxodon limnothrissa*
Docimodus johnstonii*
Fossorochromis rostratus
Hemitaeniochromis spilopterus*
Hemitaeniochromis spp.*
Hemitaeniochromis urotaenia*
Hemitilapia oxyrhynchus
Labeotropheus fuelleborni*

Lethrinops albus
Lethrinops altus*
Lethrinops auritus
Lethrinops christyi*
Lethrinops gossei*
Lethrinops 'guentheri'*
Lethrinops leptodon
Lethrinops lethrinus
Lethrinops longimanus*
Lethrinops longipinnis
Lethrinops lunaris*
Lethrinops macrochir
Lethrinops macropthallamus
Lethrinops marginatus
Lethrinops 'matumbae'*
Lethrinops microstoma
Lethrinops nyassae*
Lethrinops oculatus*
Lethrinops oliveri*
Lethrinops parvidens
Lethrinops 'round head'*
Lethrinops 'small round head'*
Lethrinops spp.
Lethrinops turneri*
Lethrinops 'yellow collar'*
Metriaclima elegans*
Metriaclima livingstonii*
Metriaclima 'patricki'*
Mylochromis 'oblique spots'*
Mylochromis anaphyrmus*
Mylochromis 'blue'*
Mylochromis 'discrete spots'*
Mylochromis ericotaenia*
Mylochromis formosus*
Mylochromis melanotaenia*
Mylochromis 'oblique band'
Mylochromis 'oblique spots'
Mylochromis 'oblique stripe yellow'*
Mylochromis 'oblique stripes'*
Mylochromis plagiotaenia*
Mylochromis sphaerodon
Mylochromis spilostichus*
Mylochromis spp.
Mylochromis 'yellow fin'*
Mylochromis 'yellow throat'*
Naevochromis chrysogaster*
Nimbochromis livingstonii*
Nimbochromis polystigma*

Nyassachromis 'deep'
Nyassachromis 'horizontal stripe'*
Nyassachromis spp. Complex
Otopharynx argyrosoma*
Otopharynx auromarginatus
Otopharynx decorus
Otopharynx productus*
Otopharynx selenurus*
Otopharynx spp.
Otopharynx tetraspilus*
Otopharynx tetrastigma
Petrotilapia spp.*
Placidochromis 'dark' henydaviesae*
Placidochromis longimanus*
Placidochromis subocularis*
Protomelas kirkii
Protomelas kirkii 'yellow throat'*
Protomelas labridens*
Protomelas marginatus*
Protomelas 'pointed snout'*
Protomelas 'red dorsal'
Protomelas similis
Protomelas 'spoted'*
Protomelas spp.
Protomelas triaenodon
Pseudotropheus cf. nomfasciatus
Pseudotropheus spp.*
Pseudotropheus tropheops spp.
Rhamphochromis 'brown'*
Rhamphochromis 'brown dorsal'*
Rhamphochromis essox*
Rhamphochromis leptosoma*
Rhamphochromis longiceps*
Rhamphochromis longiceps type*
Rhamphochromis spp.
Rhamphochromis'brown'*
Sciaenochromis alhi
Sciaenochromis benthicola*
Sciaenochromis spp.*
Stigmatochromis 'guttatus'*
Stigmatochromis spp.*
Stigmatochromis woodi*
Taeniolethrinops furcicauda*
Taeniolethrinops laticeps*
Taeniolethrinops praeorbitalis
Tramitichromis brevirostris*
Tramitichromis brevis*
Tramitichromis intermedius*
Tramitichromis lituris

Tramitichromis spp.*
Tramitichromis trilineatus*
Tramitichromis variabilis*
Trematocranus placodon
Tyrannochromis macrostoma*

Appendix C:

Offshore Haplochromine cichlids sampled by demersal trawling.

Appendix C. Offshore Haplochromine cichlids sampled by demersal trawling. Abundance codes are: r = rare, m = moderate(>10 and <51), ab = >50

Species	Abundance class	Count 10 m	30 m	50 m	75 m	100 m	125 m
Alticorpus spp.	ab	_	1	1	4	6	7
Alticorpus 'geoffreyi'	ab	_	_	2	10	10	10
Alticorpus macrocleithrum	ab	_	_	_	4	9	5
Alticorpus mentale	ab	_	1	7	10	10	10
Alticorpus pectinatum	ab	_	_	_	10	10	7
Aristochromis christyi	r	_	2	_	_	_	_
Aulonocara 'cf. macrochir'	ab	2	7	10	_	_	_
Aulonocara spp	ab	_	_	2	4	1	4
Aulonocara 'blue orange'	ab	7	8	5	1	_	_
Aulonocara 'copper'	ab	_	_	_	1	_	_
Aulonocara guentheri	ab	2	1	_	_	_	_
Aulonocara 'long'	ab	1	_	1	5	6	6
Aulonocara 'minutus'	ab	_	_	_	9	10	9
Aulonocara 'rostratum deep'	ab	_	_	2	6	4	5
Buccochromis lepturus	ab	7	6	_	_	_	_
Buccochromis nototaenia	ab	7	10	1	_	_	_
Buccochromis rhoadesi	m	1	1	_	_	_	_
Caprichromis liemi	r	_	1	1	_	_	_
Champsochromis caeruleus	r	1	1	_	_	_	_
Chilotilapia rhoadesi	ab	8	9	_	_	_	_
Copadichromis inornatus	ab	1	_	_	_	_	_
Copadichromis quadrimaculatus	ab	7	8	7	3	_	_
Copadichromis spp	m	1	1	_	_	_	_
Copadichromis trimaculatus	r	_	_	_	_	_	1
Copadichromis virginalis	ab	3	8	10	_	2	_
Corematodus taeniatus	m	3	2	1	1	_	_
Ctenopharynx nitidus	ab	8	2	_	_	_	_
Ctenopharynx pictus	m	_	_	3	_	_	_
Dimidiochromis dimidiatus	r	1	_	_	_	_	_
Diplotaxodon apogon	ab	_	_	_	8	9	9
Diplotaxodon argenteus	ab	_	_	6	10	9	10
Diplotaxodon spp	ab	_	_	_	3	2	3
Diplotaxodon 'brevimaxillaris'	ab	_	_	1	4	4	6
Diplotaxodon greenwoodi	m	_	_	_	1	1	3
Diplotaxodon limnothrissa	ab	2	_	9	10	9	10
Diplotaxodon macrops	ab	_	_	_	8	10	9
Diplotaxodon 'similis'	ab	_	_	_	1	_	1
Docimodus johnstonii	ab	2	1	4	_	_	_
Haplochromis 'sp.'	r	_	_	1	_	_	_
Hemitaeniochromis 'insignis'	ab	_	_	4	2	1	5
Hemitaeniochromis urotaenia	r	1	_	1	_	_	_
Lethrinops christyi	ab	3	1	1	_	_	_
Lehtrinops dark	ab	_	_	1	_	_	_
Lethrinops 'matumbae'	ab	_	8	3	_	_	_
Lethrinops 'deep water albus'	ab	_	_	2	4	2	5
Lethrinops albus	ab	_	_	1	1	_	2
Lethrinops altus	ab	5	7	9	5	5	7
Lethrinops spp.	ab	6	1	5	3	3	3
Lethrinops 'blue orange'	ab	_	1	_	_	_	_

Lethrinops dark	ab	3	1	2	3	1	2
Lethrinops 'deep water altus'	ab	_	_	_	3	4	3
Lethrinops 'furcifer'	ab	5	1	_	_	_	_
Lethrinops gossei	ab	_	_	1	10	10	10
Lethrinops 'grey'	ab	_	_	_	_	1	_
Lethrinops longimanus	ab	1	6	10	2	3	1
Lethrinops longipinnis	ab	8	10	10	2	1	2
Lethrinops macrochir	ab	6	_	_	_	_	_
Lethrinops 'macrostoma'	m	_	_	_	1	_	_
Lethrinops microdon	ab	2	_	1	1	1	_
Lethrinops 'minutus'	ab	_	_	7	_	_	_
Lethrinops mylodon	ab	_	3	1	_	2	_
Lethrinops 'oliveri'	ab	_	_	1	10	9	9
Lethrinops 'cf. parvidens'	m	2	2	4	_	_	_
Lethrinops polli	ab	_	_	1	10	9	5
Lethrinops 'stridei'	r	_	_	_	_	1	_
Lethrinops 'yellow chin'	ab	_	_	1	_	_	_
Mylochromis anaphyrmus	ab	8	10	10	1	_	_
Mylochromis formosus	ab	2	4	3	_	_	_
Mylochromis gracilis	ab	_	2	3	1	_	_
Mylochromis spp.	m	3	3	_	_	_	_
Mylochromis melanonotus	m	3	5	_	_	_	_
Mylochromis sphaerodon	r	1	1	_	_	_	_
Mylochromis spilostichus	ab	5	6	5	_	_	_
Mylochromis 'torpedo'	r	1	_	_	_	_	_
Nevochromis chrysogasta	m	1	_	_	_	_	_
Nimbochromis livingstonii	ab	2	1	2	4	_	_
Nimbochromis venustus	r	2	_	_	_	_	_
Nyassachromis argyrosoma	ab	8	8	2	_	_	_
Nyassachromis spp.	ab	3	2	_	_	_	_
Nyassachromis eucynostomus	ab	1	1	_	_	_	_
Nymbochromis polystigma	r	1	_	_	_	_	_
Otopharynx argyrosoma	ab	_	7	1	_	_	_
Otopharynx brooksi	ab	_	_	_	5	1	2
Otopharynx 'productus'	ab	7	1	_	_	_	_
Otopharynx decorus	ab	5	1	_	_	_	_
Otopharynx spp.	m	_	_	_	_	_	1
Otopharynx speciosus	ab	_	9	10	2	_	_
Pallidochromis tokolosh	ab	_	_	2	9	8	10
Placidochromis 'flatjaws'	ab	_	_	_	1	6	5
Placidochromis 'acuticeps'	m	_	_	_	_	_	4
Placidochromis spp.	ab	_	_	1	2	1	_
Placidochromis 'macrognathus'	ab	_	2	3	4	2	3
Placidochromis 'davisii III'	m	_	_	_	_	_	1
Placidochromis 'davisii IV'	m	_	_	_	_	_	1
Placidochromis johnstonii	r	_	1	_	_	_	_
Placidochromis 'long'	ab	_	4	8	_	_	_
Placidochromis 'platyrhynchos'	ab	_	_	_	1	9	10
Placidochromis 'cf. subocularis'	ab	6	3	_	_	_	_
Protomelas spilopterus	r	1	1	_	_	_	_
Protomelas triaenodon	r	3	_	_	_	_	_
Pseudotropheus elegans	ab	1	1	_	_	_	_
Pseudotropheus livingstonii	ab	7	3	_	_	_	_
Pseudotropheus spp.	m	_	1	_	_	_	_
Rhamphochromis spp	ab	8	10	10	10	6	5
Sciaenochromis spp.	r	1	_	1	_	_	_
Sciaenochromis alhi	ab	3	4	3	6	3	4
Sciaenochromis benthicola	ab	3	3	10	8	1	1

Sciaenochromis psammophilus	m	–	–	–	1	–	–
Sciaenochromis spilosticus	r	–	1	–	–	–	–
Stigmatochromis pholidophorus	r	1	–	–	–	–	–
Stigmatochromis woodii	ab	1	2	1	1	–	1
Stigmatochromis 'guttatus'	ab	1	–	4	5	1	2
Taeniochromis holotaenia	m	3	3	–	–	–	–
Taeniolethrinops furcicauda	ab	7	2	–	–	–	–
Taeniolethrinops laticeps	m	–	7	–	–	–	–
Taeniolethrinops praeorbitalis	ab	3	7	–	–	–	–
Tramitichromis lituris	ab	2	–	–	–	–	–
Trematocranus brevirostris	ab	–	1	8	–	–	–
Trematocranus macrostoma	r	2	–	–	–	–	–
Trematocranus placodon	ab	5	–	–	–	–	–
Total Haplochoromine species number		63	62	58	51	42	44