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Biodiversity Assessment and Conservation in Lake Tanganyika

BIOSS FINAL TECHNICAL REPORT

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Pollution Control and Other Measures to Protect Biodiversity in Lake Tanganyika (RAF/92/G32)

Lutte contre la pollution et autres mesures visant à protéger la biodiversité du Lac Tanganyika (RAF/92/G32)

Le Projet sur la diversité biologique du lac Tanganyika a été formulé pour aider les quatre Etats riverains (Burundi, Congo, Tanzanie et Zambie) à élaborer un système efficace et durable pour gérer et conserver la diversité biologique du lac Tanganyika dans un avenir prévisible. Il est financé par le GEF (Fond pour l'environnement mondial) par le biais du Programme des Nations Unies pour le développement (PNUD)

The Lake Tanganyika Biodiversity Project has been formulated to help the four riparian states (Burundi, Congo, Tanzania and Zambia) produce an effective and sustainable system for managing and conserving the biodiversity of Lake Tanganyika into the foreseeable future. It is funded by the Global Environmental Facility through the United Nations Development Programme.



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EXECUTIVE SUMMARY

1. Lake Tanganyika is one of the world's biodiversity 'hotspots'. Its diversity is threatened by the impact of human activity in the lake and its catchment. The Lake Tanganyika Biodiversity Project (LTBP) was conceived as a means of providing a regional framework for the management of the lake and protection of its biodiversity. The Biodiversity Special Study (BIOSS) provided technical advice to the project on techniques for biodiversity survey design and assessment and on current management approaches used for biodiversity conservation. We also undertook a range of training and capacity building activities in support of LTBP objectives.
2. The main aim of the BIOSS was to support the development of a strategic action plan (SAP) to manage Lake Tanganyika. The aim of the strategic action plan is "to provide for the regional management of Lake Tanganyika to enable the sustainable management of biodiversity and the livelihoods of present and future generations of lakeside communities."

The specific objectives of the SAP that the BIOSS study addressed most directly were:

- "Define and prioritise the management actions required to conserve biodiversity of Lake Tanganyika"
- "Enable the Lake Basin Management Committee to provide guidance to the international community on the needs of the Lake Tanganyika region in terms of biodiversity conservation and sustainable use of resources".

To achieve these aims the BIOSS had four key objectives:

- Review current levels of biodiversity in Lake Tanganyika;
- Identify the distribution of major habitat types, with particular focus on existing and suggested protected areas;
- Suggest priority areas for conservation, based on existing knowledge and recommendations from other SS and supplemented by additional survey work where necessary; and,
- Develop a sustainable biodiversity monitoring programme.

3. This technical report provides the results of research activities directed towards addressing these objectives. We review the concepts and processes that led to the choice of methodology, and validate that methodology (Chapter 2). We present a summary analysis of current knowledge about biodiversity relevant to conservation based on analysis of available secondary information (Chapter 3), and the results of surveys conducted by the BIOSS team from 1997-1999 (Chapter 4). These data are used to provide an improved basis for conservation decision-making (Chapter 5). We conclude with a summary of recommendations for approaches to conservation, management action, monitoring, and research priorities (Chapter 6). The report also provides an extensive bibliography (Chapter 7) and an archive for important data (Chapter 8).
4. Development of suitable survey approaches, yielding standardised protocols for comparative assessments of biodiversity, occupied a considerable part of the BIOSS programme. We paid attention to process considerations as well as the delivery of technical outputs in the form of survey data. Thus, we adopted practices that were implemented with the full participation of local scientists and technical assistants. Teams from Burundi, DR Congo, Tanzania and Zambia all participated in the design and testing of the survey methods. This has ensured a high level of ownership and understanding of the survey methodology, which should ensure it is used in future survey activities.
5. Most taxa in the lake are not sufficiently well known taxonomically to form the basis for large-scale survey activities. The main techniques developed were therefore standardised protocols for sampling the very diverse fish community, as total biodiversity surrogates. Three fish-survey techniques were developed for the project, two SCUBA based techniques – Stationary visual census (SVC) and Rapid visual census (RVC) - and

standardised protocols for gillnet surveys. These techniques were carefully assessed for sampling bias, complementarity and minimum required sampling size. We also developed protocols for sampling molluscs. For future surveys that aim to characterise species richness in areas to be compared for conservation prioritisation we recommend the following minimum sampling sizes and combination of survey techniques:

- RVC – 40 replicates per survey stratum (e.g. area between 5 and 15 m depth);
- Gillnet – 60 night-time sets with 60m multimesh nets per survey area;
- Mollusc transects – 30 per survey stratum (chosen depth-habitat combination); and,
- The SVC technique may be more useful for monitoring surveys, as it covers less ground and takes longer, but may be more precise.

6. Estimates of species richness and diversity are sensitive to sampling size. We recommend use of Shannon-Weiner estimates of diversity in preference to Simpson's index as it gives more consistent results from undersampled areas. We also recommend Chao's Incidence-based Coverage Estimator (ICE) and the Michaelis-Menton (Means) estimation procedures for species richness.
7. Most of the work done in Lake Tanganyika prior to this project was not undertaken for the purposes of conservation planning so it is not standardised for this purpose. This inevitably limits its value in comparative analysis, or as baseline data to assess changes over time. This data does, however, provide a rich archival source, which, through the efforts of BLOSS in collating some of it into a relational database, is being made available to regional agencies as a powerful tool for conservation planning and research purposes.
8. Prior to the BLOSS study, there was a lack of information on aquatic habitats and their associated biota in the areas within or adjacent to the terrestrial-based National Parks (Rusizi, Gombe, Mahale, Nsumbu). BLOSS developed a survey procedure and built up capacity to implement surveys that utilised regional expertise and minimised dependence on external inputs.
9. The habitat surveys established that the areas adjacent to the existing terrestrial protected areas, whether they are currently protected as aquatic zones or not, contain the full range of littoral habitat types, including emergent macrophytes, submerged macrophytes, stromatolite reefs, shell beds and all combinations of soft and hard substrates. They do not necessarily provide the only or best examples of such habitat types, but have the advantage of existing conservation focus. Thus, the fundamental criterion for a protected area network – that it should contain good examples of all habitat types (and by inference the associated biota) – is fulfilled by the existing network.
10. The highest biodiversity, in terms of number of species, is situated in the sub-littoral zone (down to 40 m). We find that a high percentage of this biodiversity is ubiquitous in its distribution, but that there are limited number of taxa with spatially restricted distributions. 73% of described lacustrine fish (90% of species recorded in BLOSS surveys) were found in waters adjacent to existing national parks. A conservation strategy based primarily on maintaining and extending the functions of the existing terrestrial parks is therefore recommended.
11. Fish communities on rocky substrates are more diverse than those on sandy ones, and undisturbed or relatively pristine habitats support higher diversities than those areas close to population centres and subject to disturbance from fishing, pollution and sedimentation. These differences are also evident in comparing species richness measures. The analysis confirms the high diversity of the waters off existing parks, and highlights other areas, such as Pemba, Bangwe, Luhanga, in Congo, and Lufubu and Chisala in Zambia which are potentially rich sites. The latter are river mouth areas adjacent to Nsumbu National park, and may be worthy of some form of protection.
12. BLOSS has based its conservation strategy advice mainly in terms of protected areas. This reflects the original LTBP project document, which went as far as to specify the creation of additional National Parks, as well as strengthening the management of

existing ones. We have attempted to identify the areas of greatest diversity and sought to establish which combination of these would give the greatest level of protection to Lake Tanganyika's biodiversity. It is recognised however, that protected area status is only one option, and that a wider approach to lake management is likely to be critical if the strategy is to be successful. We therefore discuss additional strategies such as coastal zone management and integrated conservation and development.

13. As pressure on Lake Tanganyika's resources increases with population growth, threats to the lake's biodiversity are likely to increase in intensity and effective conservation measures will be essential if the integrity of aquatic ecosystems and the ecological services they provide are to be maintained. The existing system of national parks contributes significantly to protection of biodiversity in Lake Tanganyika, including representation of all the main aquatic habitat types and a high proportion of fish and mollusc species. But the parks are isolated, constitute only a fraction of the coastline and there are no guarantees that the populations that they support would be viable if surrounded by hostile environments. The feasibility of achieving a more comprehensive level of protection through an extension of the present parks network is highly questionable. For this reason we have highlighted the alternative of a Coastal Zone Management strategy, which combines the goals of biodiversity conservation with development and stakeholder participation.
14. LTBP had a strong technical focus, providing essential baseline information for the first management plan for the lake. The basis for scientific monitoring and underpinning of management has been established under LTBP, but the wider skills in communication, joint planning, co-operation between different ministries/disciplines and management are still required. Throughout our report, we have stressed the need to consider process issues as well as deliver technical outputs. If the international community still values this unique lake, we would recommend ongoing support that concentrates more on building the institutional capacity needed to ensure sustainable development of this biodiverse resource. We would also recommend a critical analysis of the costs and benefits of such conservation and explicit development of management approaches that will assist in ensuring that benefits of conservation flow to those who live around the lake, while the costs are borne by all who value it.

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1. INTRODUCTION

1.1 Lake Tanganyika and its biodiversity

Whereas most modern lakes were formed by glaciation within the last 12,000 years and have had a history of frequent water chemistry fluctuations and/or desiccation (Wetzel 1983), the African Rift Lakes are geologically long-lived. Dating back about 12 million years (Cohen et al 1993), Lake Tanganyika is the oldest of the African Rift Lakes, and behind Lake Baikal in Russia, it is the second-oldest and second-deepest lake in the world. Four countries bound Lake Tanganyika's 1,838 km perimeter: Burundi (controlling 9% of the coastline); Democratic Republic of Congo (administering 43% of the coastline); Tanzania (governing 36% of the coastline), and Zambia (claiming 12% of the coastline) (statistics from Hanek et al 1993). Lake Tanganyika drains a catchment area of about 220,000 km². It is fed by numerous small and two major influent rivers: the Rusizi draining Lake Kivu to the north, and the Malagarasi, draining Western Tanzania south of the Victoria Basin. Only a single outlet, the Lukuga River, drains Lake Tanganyika.

This ancient and nearly closed ecosystem harbours a remarkable fauna. While all of the African Great Lakes host world-famous species flocks¹ of cichlid fish, Lake Tanganyika, in addition to its species flocks of cichlid fish (250+ species), also hosts species flocks of noncichlid fish (145+ species) and invertebrate organisms², including gastropods (60+ species), bivalves (15+ species), ostracodes (84+ species), decapods (15+ species), copepods (69+ species), leeches (20+ species), and sponges (9+ species) among others (Coulter 1994). Lake Tanganyika, with more than 1,300 species of plants and animals is one of the richest freshwater ecosystems in the world. More than 600 of these species are endemic (unique) to the Tanganyika Basin and in many cases these taxa also represent endemic genera and sometime endemic families. With its great number of species, including endemic species, genera and families, it is clear that Lake Tanganyika makes an important contribution to global biodiversity.

One might expect that an abundance of species coexisting for a long period of time in a nearly closed environment would show interesting evolutionary patterns and behaviours. They do, including: species that are morphologically similar but genetically distinct, species that are genetically similar but morphologically distinct, species that are evolving robust armour in response to predation, species that diversified in jaw morphology in order to exploit every available trophic niche, and species that have adopted complex reproductive and parental care strategies, including nesting, mouth-brooding and brood parasitism (See Coulter (1991) for a review of these and other topics). With its numerous species exhibiting complex and derived patterns and behaviours, Lake Tanganyika is a natural laboratory for investigating ecological, behavioural and evolutionary questions.

While the cichlid species flocks of Lake Tanganyika are world famous, three non-cichlid species have drawn even more human interest. Two clupeid (sardine) species and *Lates stappersi* dominate the lake's biomass and constitute the target of the lake's artisanal and industrial fisheries. The sardine species, like their marine relatives, are small, numerous, short-lived and highly fecund. The *L. stappersi* is a large predator. The lake wide, annual harvest yields of these fish stocks has been estimated at 165,000 – 200,000 tonnes per year, volumes that translate into earnings of tens of millions of dollars (Reynolds 1999), making them an important part of the ecosystem and the economy.

In addition to being a global repository of biodiversity, Lake Tanganyika plays an important role in the economies of the riparian countries. Tanganyika is a source of fresh water for drinking and other uses. Fish provide a major source of protein in the local diet and the

¹ Species flocks are groups of closely-related organisms which are endemic to a circumscribed area and possess great species richness compared to other occurrences of the group elsewhere.

² These invertebrate species numbers are certainly significantly underestimated, as these groups in general have received relatively little attention from taxonomists and in addition, much of the Tanganyikan coast has not been adequately explored. Nonetheless, it is clear that invertebrates in other lakes do not show nearly these levels of diversity.

fishing industry, including harvesting, processing and marketing. Fishing-related occupations are a source of income and employment for more than 1 million people. Transport is another major industry on the lake, which serves as a super-highway connecting people and cargo within and between the riparian countries.

In spite of its importance to global biodiversity and to the economies of the region, Lake Tanganyika is threatened by several potentially disastrous environmental problems. These include: pollution from untreated industrial and domestic wastes, sediment pollution as a result of deforestation, and over fishing or fishing with inappropriate or destructive gears. Concern for Lake Tanganyika's future resulted in the First International Conference on the Conservation and Biodiversity of Lake Tanganyika in Bujumbura in 1991, where regional and international scientists gathered to discuss Tanganyika's riches and the burgeoning threats against it (Cohen, 1991). Ultimately these efforts resulted in the Global Environmental Facility (GEF) initiative for the "protection of biodiversity" through "a coordinated approach to the sustainable management of Lake Tanganyika." The Lake Tanganyika Biodiversity Project was funded by the United Nations Development Program (UNDP), executed by the United Nations Office of Project Services (UNOPS), and implemented by a UK-based consortium consisting of the Natural Resources Institute (NRI), the Marine Resources Assessment Group (MRAG), and the Institute of Freshwater Ecology (IFE).

1.2 The Convention on Biological Diversity and its implementation on Lake Tanganyika

1.2.1 The Convention on Biological Diversity

The Convention on Biological Diversity (CBD) was one of the outputs of the 1992 UN Conference on Environment and Development in Rio de Janeiro (UNEP, 1994). The CBD or 'Convention' is a commitment by the nations of the world to conserve biological diversity. Over 200 countries have signed the Convention, including Burundi, Democratic Republic of Congo, Tanzania, Zambia and the UK. All signatories recognise that biodiversity and biological resources should be conserved for reasons of ethics, economic benefit, and, in the long term, human survival. The objectives of the CBD are:

- Conservation of Biological Diversity
- Sustainable use of its components
- Fair and equitable sharing of the benefits arising out of the utilisation of genetic resources

The Convention has agreed the following definition of 'biodiversity', which is the broad definition used by the Biodiversity Special Study and Lake Tanganyika Biodiversity Project:

"'Biological Diversity' means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems "

(Article 2, Convention on Biological Diversity, UNEP, 1994)

The Convention recognises a very broad range of concerns linked to loss of biodiversity, and provides the policy and legal framework for national and international initiatives to conserve the world's natural resource systems. Glowka *et al.* (1994) provide a detailed overview of the articles of the Convention, and Allison (1998) reviews their relevance to LTBP.

1.2.2 The Global Environment Facility

The Global Environment Facility is a financial mechanism and policy instrument designed specifically to assist developing countries in meeting their obligations as signatories to international environmental agreements. Specifically, the GEF provides grants to assist developing countries to address environmental problems that transcend international borders in four areas: global climate change, pollution and overexploitation of international waters,

destruction of biological diversity, and depletion of the ozone layer. It will also fund activities associated with preventing or reversing land degradation, providing this has an impact on one of this four focal areas.

GEF funds and programmes are administered both by the UN Environment Programme and the UN Development programme, thereby ensuring that both environmental and development issues are represented in its programmes and projects. The funding comes from the World Bank, which is also involved in administering the programme (for example, the Lake Malawi/Niassa GEF programme was implemented through the World Bank).

The GEF has a number of focal areas, within which are operational programmes that specify objectives related to areas identified as priorities for environmental management. The Lake Tanganyika Biodiversity Project was funded under the 'International Waters' programme, although it had clear links to the 'Biological Diversity' programme. The two operational programmes within these focal areas that are most relevant are 'Biodiversity of Coastal, Marine and Freshwater Ecosystems' and 'Waterbody-based programme'. A new focal area on 'The Land-Water Interface' is also relevant.

In formulating our contributions to the project, we have been careful to work as much as possible to the operational strategies specified by the GEF (see Allison, 1998).

1.3 LTBP Project goals and the Biodiversity Special Study

LTBP project goals were initially specified in the LTBP project document and Inception Reports (LTBP 1995, 1996). These goals have been modified as the GEF operational strategies have changed (Hodgson, 1997). The goals and objectives indicated here are taken from the 1997 Project Performance Evaluation Report (LTBP, 1997)

1.3.1 Project goal and purpose

"The goal of the project is the protection of biodiversity in Lake Tanganyika. This will be achieved via the project purpose, which is to create a co-ordinated approach to the sustainable management of Lake Tanganyika. This in turn will be accomplished by increasing institutional capacity within the riparian states to monitor and manage threats to the lake."

It should be noted that the project purpose is stated in terms of a **process**, rather than an **output**: "to create a co-ordinated approach to management ... by increasing institutional capacity". Scientists are generally less comfortable with the notion of 'process' and tend to focus on delivering outputs by the most efficient means possible (Shumway, 1999). In development work, it is recognised that outputs are linked very closely to process – in other words whether you achieve longer term, larger-scale goals depends as much on *how* you moved towards your goals as on *what* you produced (Cornwall, 1993; Mosse et al., 1998).

This report focuses mostly on outputs – the analysis of data on biodiversity distributions to inform conservation management. The BIOS team, however, has been aware of the importance of process, so we have included some documentation of the rationale for our approach, and have reflected on our experience in developing and implementing this approach (see Chapters 2 and 6).

1.3.2 LTBP Project Objectives

The LTBP has six immediate objectives (LTBP, 1997):

- Establish a regional long-term management programme for pollution control, conservation and maintenance of biodiversity in Lake Tanganyika
- Formulate a regional legal framework for co-operative management of the lake environment.
- Establish a programme of environmental education and training for Lake Tanganyika and its basin.

- Establish tested mechanisms for regional co-ordination in conservation management of the Lake Tanganyika Basin.
- In order to produce a full Strategic Plan for long-term application, some specific studies need to be undertaken. These special studies will also add to the understanding of the lake as a whole, and in some cases, provide the baseline and framework for long-term research and monitoring programmes.
- The implementation and sustainability of the Lake Tanganyika Strategic Plan and incorporated environmental management proposals.

1.3.3 The Special Studies

Objective 5 of the LTBP project (Section 1.3.2) identifies the need for special studies to add to the understanding of the lake and provide the baseline and framework for long-term research and monitoring activities. The following table draws together the main objectives or aims of each of the other special studies.

Table 1.1 Special studies and their main aims

Special Study	Aims
BIOSS	<p><i>Four key objectives:</i></p> <ul style="list-style-type: none"> • review current levels of biodiversity in Lake Tanganyika; • identify the distribution of major habitat types, with particular focus on existing and suggested protected areas; • suggest priority areas for conservation, based on existing knowledge and recommendations from other SS and supplemented by additional survey work where necessary; and, • develop a sustainable biodiversity monitoring programme.
FPSS	<p><i>Two main aims:</i></p> <ul style="list-style-type: none"> • to understand the potential impact of different fishing practices employed in the littoral zone on fish biodiversity and • to understand the importance of these artisanal fishing practices to riparian communities
POLSS	<p><i>Main goal:</i> To identify the main sources of pollution, to determine where and how such pollution is negatively impacting biodiversity, and establish a monitoring programme for pollution in the lake.</p>
SEDSS	<p><i>Aim</i> To understand the links between catchment factors which affect erosion (rainfall, vegetation, slope, soil etc.), to understand how and in what quantity these erosion materials are transported to the lake and to attempt to understand their impacts on the lake ecosystem.</p>
SESS	<p><i>Principle tasks:</i></p> <ul style="list-style-type: none"> • to provide an understanding of current livelihood strategies and SE practices around the Lake and its catchment area, and • to suggest ways in which alternative livelihood strategies can be introduced while changes in current practices, which may be detrimental to biodiversity, are encouraged.

We have used a Venn diagram (Figure 1.1) to illustrate the relationship between the biodiversity study and each of the other special studies, and in turn the relationship between the studies and the other major components of the entire project, i.e. training, strategic action programme and the legal convention.

As can be deduced from the diagram, all project activities are designed with the overall aim of informing the Strategic Action Programme (SAP) for the management of Lake Tanganyika. Then in turn, the convention gives the ultimate authority for the SAP to be managed and implemented. The BIOSS is responsible for developing appropriate field methods for the assessment of impacts on biodiversity of Lake Tanganyika. These methods can then be applied in collaboration with other special studies in the assessment of the impact on diversity of pollution, sedimentation and fishing practices. A review of the current status of biodiversity

in the lake (Allison *et al.*, 1996; Patterson and Makin, 1998) informed and guided the field programme and development of future activities.

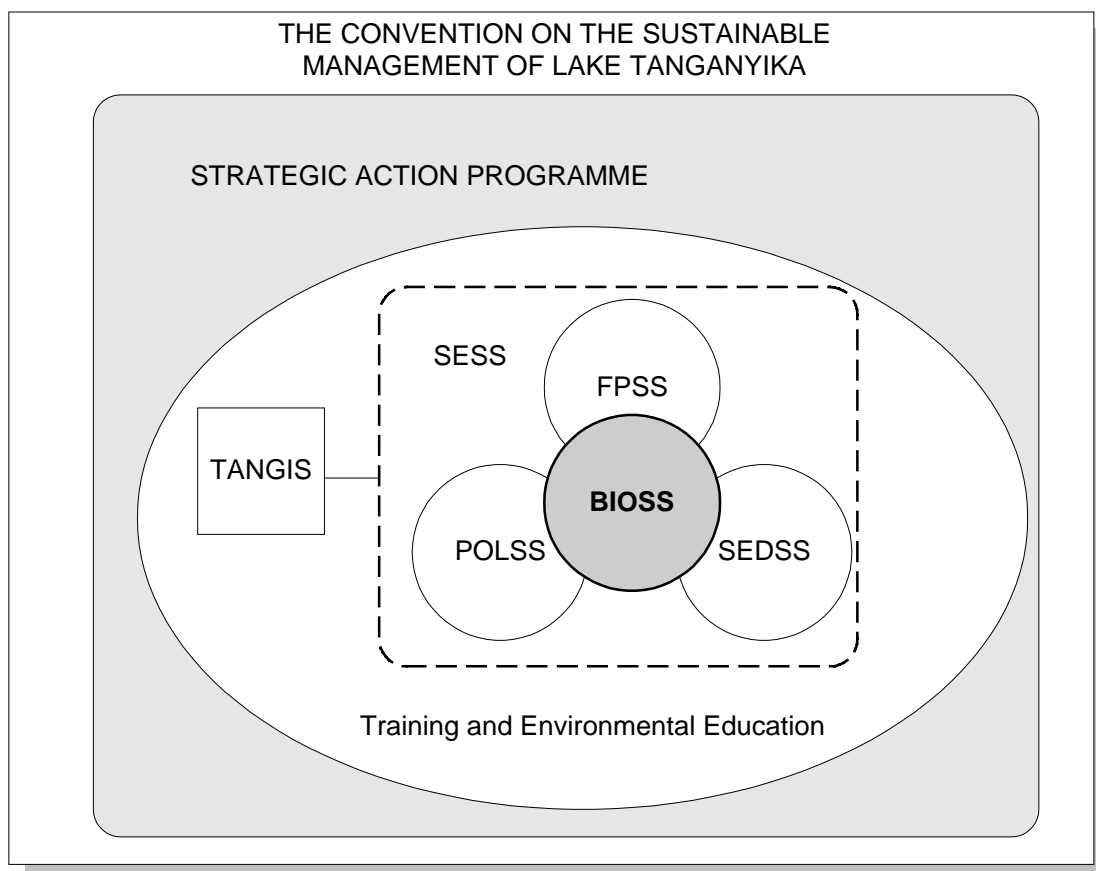


Figure 1.1 Venn diagram illustrating the relationship between BIOSS, the other special studies and other major components of LTBP

1.4 Aims and Objectives of BIOSS

The main aim of the BIOSS is to support the development of the strategic action plan (SAP) to manage Lake Tanganyika. The aim of the strategic action plan is “to provide for the regional management of Lake Tanganyika to enable the sustainable management of biodiversity and the livelihoods of present and future generations of lakeside communities.”

The specific objectives of the SAP that this study addresses most directly are:

- “Define and prioritise the management actions required to conserve biodiversity of Lake Tanganyika”
- “Enable the Lake Basin Management Committee to provide guidance to the international community on the needs of the Lake Tanganyika region in terms of biodiversity conservation and sustainable use of resources”.

To achieve these aims the BIOSS has four key objectives:

- Review current levels of biodiversity in Lake Tanganyika;
- Identify the distribution of major habitat types, with particular focus on existing and suggested protected areas;
- Suggest priority areas for conservation, based on existing knowledge and recommendations from other SS and supplemented by additional survey work where necessary; and,
- Develop a sustainable biodiversity monitoring programme.

Objectives 1, 3 and 4 would ideally have been carried out in close consultation with the other SS teams, but the desired level of integration was difficult to achieve in practice. Objective 3 in particular is perhaps best regarded as a cross-sectoral activity. This report's recommendations are thus framed largely in terms of biodiversity criteria for conservation prioritisation. These criteria were addressed during the Strategic Action Programme process, together with information on threats and feasibility of conservation supplied by other special studies.

This technical report provides the results of research activities directed towards addressing these objectives. We present a summary analysis of current knowledge about biodiversity relevant to conservation based on analysis of available secondary information (Chapter 3), and the results of surveys conducted by ourselves (Chapter 4) aimed at providing an improved basis for conservation decision making (Chapter 5). We also review the concepts and processes that led to the choice of methodology, and validate that methodology (Chapter 2). We conclude with a summary of recommendations for action, monitoring, and research (Chapter 6).

2. DEVELOPING A BIODIVERSITY ASSESSMENT STRATEGY FOR LAKE TANGANYIKA

The aims of this chapter are to provide an overview of the rationale and analysis that has informed our choice of methodology; to assess the sources of bias and error in the chosen sampling methods, and to provide an evaluation of the methods adopted. The output of this process is the data for information review and survey programmes analysed in Chapters 3 and 4. Those analyses, in turn, are used to inform options for conservation management (Chapter 5).

2.1 Assessing Biodiversity

The science of biodiversity assessment is new. The term 'biodiversity' did not come into common usage until the late 1980s (Wilson, 1989). To date, most biodiversity assessments for the purposes of conservation and resource management have taken place in terrestrial systems. Despite accumulating experience, procedures for biodiversity assessment in forests, grasslands etc are far from standardised, and vary according to objectives of the work, expertise and resources available, and the philosophy and approach of the teams doing the surveys (Jermy et al., 1995; Purvis and Hector, 2000). The terrestrial biologist therefore has a large range of techniques and approaches to choose from. These techniques have been evaluated and tested over the last decade. In aquatic systems there is much less experience of conservation-related biodiversity assessment surveys. The sciences of marine ecology and limnology provide sets of standardised procedures for sampling and analysis, but these have seldom been developed with biodiversity assessment in mind. When one considers the unique environments of the African Great Lakes, there is very little prior experience on biodiversity assessment. The LTBP and Lake Malawi Biodiversity Projects, both GEF projects with a goal of producing Lake Management Plans, are the first large-scale programmes to require extensive biodiversity assessments in this type of environment.

Most previous work on Lake Tanganyika's biota falls within five major categories: fisheries biology, biological limnology, basic taxonomy and systematics, evolutionary biology, and behavioural and descriptive ecology; Coulter's (1991) classic book integrates all five categories. There is some recent work on discussion of appropriate conservation measures for Lake Tanganyika (Coulter and Mubamba, 1993; Pendleton and Van Breda, 1994; Cohen, 1994; Coulter, 1999), but this work, which is laudably concerned with highlighting conservation issues, has not been in a position to back up the various claims made with standardised, comparable data sets.

Biodiversity assessment draws from the professional and academic traditions of all these sciences, but also adds elements from applied quantitative ecology and conservation biology. Particularly relevant are recent literatures on assessing adequacy of sampling effort, means of summarising biodiversity data for comparative analysis, and the use of complementarity analysis for reserve planning and design (reviewed in Coddington and Colwell, 1994; Margules and Pressey, 2000 and Southwood and Henderson, 2000; Chapter 13).

2.2 Determining information needs: an objectives-driven approach

From the BLOSS objectives we identified certain key questions that required analysis of existing data, and the collection of new data:

- How is biodiversity distributed within the lake?
- Is there any evidence for change in biodiversity distribution over recent time (e.g. last 50 years), possibly associated with anthropogenic disturbance of the lake environment?
- If biodiversity needed protecting, which areas would you protect?

In developing a methodology for biodiversity assessment, a fundamental question is how much do you need to know about biodiversity in order to manage or conserve it successfully? In addressing this question, we have been guided by two observations:

1. *Biodiversity in Lake Tanganyika is increasingly threatened.*

If it is accepted that threats to biodiversity are increasing (Cohen, 1991; Cohen *et al.*, 1996; Coulter and Mubamba, 1993; Coulter, 1999), this is justification enough for conservation action. We know the direction of change, and there is consensus that it is not a favourable one. The problem is therefore one of finding a way to reverse the change. Dealing with the causes of extinction and resource degradation is more important than documenting the process precisely. Ideally, a sound scientific understanding of the nature and rate of change supports incisive and cost-effective intervention, but too often, the effort needed to provide this understanding delays action until it is too late.

2. *Information is needed to help choose from a set of possible responses to the threats to biodiversity.*

Sufficient information must be available to choose a suitable course of action for conservation if resources are not to be squandered tackling low-priority problems. Conservation action needs to address three main issues:

- What are the most important or valuable areas, habitats or species to conserve?
- What are the most threatened areas, habitats or species?
- What conservation actions are most easily achievable and have least adverse development impacts?

The Transboundary Diagnostic Analyses carried out in 1998 and 2000 (LTBP, 1998; 2000) sought to prioritise conservation actions on the basis of these three broad criteria.

BIOSS addresses mainly the first of these conservation-related issues: which areas, habitats and species are most valuable in conservation terms? Pollution, Fishing Practices and Sediments special studies have identified the nature and degree of threats to the lake's biodiversity. Socioeconomics and Environmental Education special studies have addressed mechanisms, and (at least qualitatively) social and economic costs and feasibility of threat-mitigation and conservation action. Together, these studies informed the SAP.

With the above two observations in mind, the BIOSS strategy has been to combine analysis of existing information on the distribution of biodiversity in Lake Tanganyika with surveys of areas identified as being potential candidates for conservation. These are mainly areas where conservation action is likely to be least costly, in social and economic terms, and where institutional and administrative structures are already in place to facilitate conservation activities. The areas that best fulfil these criteria are those within, or adjacent to, existing terrestrial national parks – Rusizi delta in Burundi, Gombe Stream and Mahale Mountains in Tanzania, and Nsumbu National Park in Zambia. Survey activities were thus targeted at these areas, with additional work in areas known to be threatened, such as those in the vicinity of the Lake's major human settlements – Bujumbura, Kigoma, Mpulungu and Uvira. The areas we surveyed are indicated in Figure 2.1.

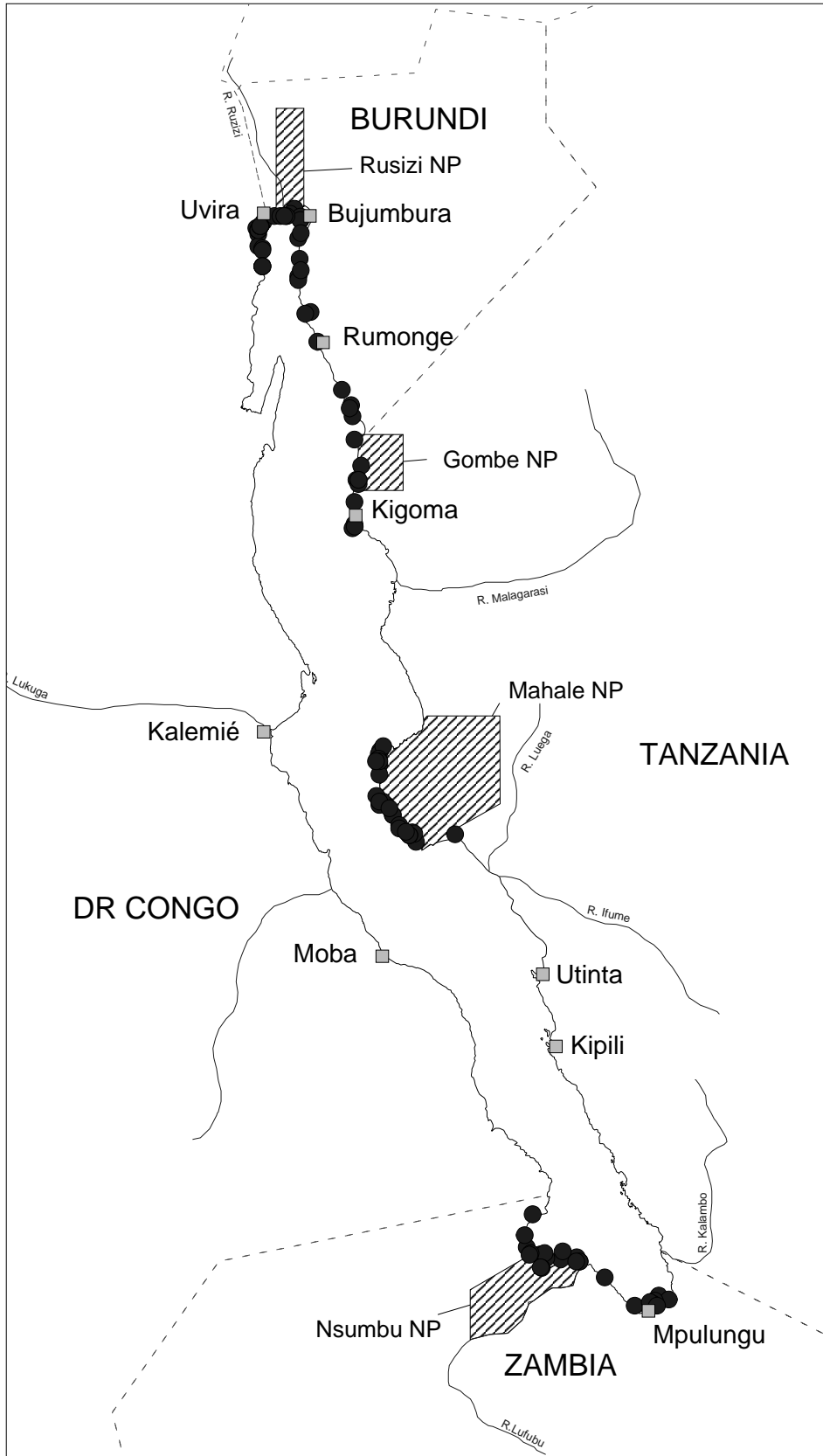


Figure 2.1 Map locating all BIOS S survey sites

2.3 Information review and organisation

The first part of any biodiversity programme is to review existing information: its quality, availability and relevance to conservation. Answers are required to the most basic questions about the lakes' biodiversity:

- Which are the most diverse areas?
- Where are the major barriers to species distributions, or to gene flow between populations of species?
- Which species are associated with which habitats?
- Which species distributions or abundances have changed due to environmental degradation or unsustainable resource use?

2.3.1 Baseline review and 'Literature Database'

A literature-based baseline review was used to provide an initial overview of the type of information available (subsequently published under editorship of Patterson and Makin, 1998). The baseline review revealed that much of the available information was in the form of scattered observations from exploratory collecting expeditions and notes from the aquarium fish trade. There was little published survey work that adhered to basic ecological survey principles (e.g. Sutherland, 1996). This is not a criticism of previous work – it was undertaken with different objectives in mind – but an indication that most of the published literature can provide only species 'presence' data. Absence can only be inferred if adequate and comparable sampling was undertaken by all surveys. Subject to errors in identification, failure by some authors to identify collecting or sampling areas precisely, and the limited distribution of survey effort, the data do provide species-distribution maps that can be analysed to infer 'hotspots' with reference to criteria such as endemism, higher-taxon diversity and range limitations.

There are, however, some datasets that have been designed specifically to assess species distributions and relative abundances (the most common components of biodiversity indices) for comparative purposes. There is an extensive database on the lake's pelagic fisheries (reviewed by the FAO/FINNIDA Lake Tanganyika Research Project), a historical data series of gillnet catches in Nsumbu Bay, Zambia (Coulter, 1991), surveys of the impact of sediments on littoral fish, ostracods and molluscs in the northern part of the lake (Cohen et al., 1993; Alin et al., 1999), and a series of fish surveys, also in the northern part of the lake (Ntakimazi, 1995, CRRHA³).

It became obvious that a useful analytical synthesis of this information could only be achieved through creation of a relational database. The 'literature database' (Pearce and Holden, 1999) was designed to be sufficiently flexible to include even the most anecdotal of information, but to provide sufficient structure to allow analysis of recorded species by location, major habitat groupings, trophic guilds and year and method of survey. Details of database structure are given in the SOP⁴ document (Allison *et al* 2000), together with procedures for its management and update within the region. It was specifically designed to be updated and used beyond the life of the current project, with no further input from outside the region except for the usual courtesy (and legal obligation under Articles 17 and 18 of the Convention on Biological Diversity) for foreign scientists to supply riparian country institutions with publications resulting from work done in the region. After initial data entry in London to help develop the structure, subsequent data entry was co-ordinated by Prof. G. Ntakimazi in Bujumbura, Burundi. Preliminary analysis of information collated to date is given in Chapter 3 of this report.

Procedures for analysis, updating and maintenance have been developed, and are detailed in the SOP document (Allison *et al.*, 2000). The database was an ambitious activity for BLOSS to undertake in addition to a regional field programme, both in terms of the scale of the task and the technical skills required. As a result, at the close of BLOSS Professor Ntakimazi in

³ CRRHA – Centre Regional de Recherche en Hydrobiologie Applique

⁴ Standard Operating Procedures for BLOSS

Burundi and MRAG in London jointly maintain the master database. Much of the relevant literature is located in Bujumbura, while the technical support for the analysis and development of the database is carried out from London. It is hoped that the considerable training needed to ensure the database can be sustained in the region will be a component of the future stages of the LTBP project.

2.3.2 The survey database

A second relational database, also programmed in Microsoft Access, was established to manage survey data generated by the BIOS S special study and subsequent monitoring activities (Jones, 1999). The survey activities and database procedures were designed to provide for continued survey activities in the lake, and to be sufficiently flexible to allow addition of new methods for other taxonomic groups once knowledge of their basic taxonomy and ecology is sufficient to allow their inclusion.

Each national team was responsible for updating the database with information on surveys conducted within their national waters. The database has the facility for each country to send regular updated national data files to a central location, where a master copy of a regional (whole-lake) database will be maintained. The updated regional database should then be returned to each riparian country. Further details on database structure and procedures are given in the BIOS S SOP where procedures for updating both national and a master regional database have been implemented are also described.

As with the literature database, the technical knowledge is insufficient to maintain this system in the region. Therefore, a similar arrangement whereby MRAG and Professor Ntakimazi continue to jointly maintain the survey database has been established. The analyses presented in this report are based on data held in these two databases. Both databases are linked to LTBP's Geographical Information System, TANGIS (Mills *et al.*, 1999).

2.4 Analysis of institutional capabilities, costs and logistical feasibility of biodiversity assessment

Conservation is a management activity. Institutions carry out management activities. The nature and scope of any conservation-related activity will, in part, be determined by institutional capability. A strong institutional capability for conservation research is more useful if it is allied to a capacity to act on research recommendations (Allison, 1998). An assessment of institutional capability is therefore an important pre-requisite to developing a biodiversity research, monitoring and management programme within LTBP.

Institutions may be formal - government agencies, research organisations, universities, schools, NGOs etc. - or they may be informal and traditional - village committees or co-operatives of resource users. Institutions can also be described as the social 'norms, standards and practices' that define or determine human activities (Ostrom, 1990). Cultural traditions, religions, and social networks and hierarchies are all forms of human institutions. All could provide a focus for involvement of conservation-related activities. Recent conservation practice in sub-Saharan Africa and elsewhere has been directed towards working more with informal, 'local' or 'community' institutions, especially in wildlife, forest and fisheries management (McNeely, 1995; Pinkerton and Weinstein, 1995; Western and Wright, 1994).

The technical special studies (Biodiversity, Pollution, Sediments) have, however, focused most of their activities on formal institutions. It is the formal institutions that have been involved in research for management, and that have been the focus of training and institutional capacity-building activities. The GEF have been criticised for a bias towards these formal institutions (Edwards and Kumar, 1998). Within the wider LTBP project, there has been awareness of the need to involve communities and other informal institutions, (Roland and Trudel, 1998). These types of institution have been involved in the project, most frequently in the training and environmental education component, socio-economic study and to some degree the fishing practices species study.

The capabilities, resources and needs of the formal institutions with a potential role in conservation research and management in the Lake Tanganyika catchment were assessed in 1996 (Allison *et al*, 1996). The assessment was conducted through visits to lake-shore laboratories and the offices of government institutes involved in water, land, fisheries and wildlife/environmental resources management. Key research institutes, including the Universities of Dar es Salaam and Zambia, were also visited. As well as obtaining profiles of professional staff and their interest and ability to participate in the project, the visit assessed requirements for equipment, technical support and specialist training. This assessment was used to determine a strategy for developing the research and monitoring capabilities required as a basis for improved conservation planning and action.

Institutional capability to undertake biodiversity assessments was limited. This is not surprising – there was no previous institutional mandate to undertake this type of work. One of LTBP’s main functions was to ‘mainstream’ biodiversity issues in the mandate of relevant government departments, in order to assist the riparian countries from fulfilling their obligations as signatories of the Convention on Biological Diversity. BLOSS strategy has therefore been to involve the relevant institutions in the development of methods for biodiversity survey and monitoring, and assist these institutions in developing teams that could realistically be expected to function given the constraints identified.

The main participating institutions are indicated in Table 2.1. These are the institutions from which BLOSS survey team members were drawn directly. A full list of individuals and institutions involved in the BLOSS special study in consultative, administrative and training roles is given in the acknowledgements (page IV).

Table 2.1 National institutions participating in BLOSS

Country	Institution
Burundi*	University of Burundi, Department of Biology, Department of Mathematics and Computer Sciences, Bujumbura
	Departement de L'eau, Peche et Pisciculture
	Institut National pour l'Environnement et Conservation de la Nature (INECN)
Democratic Republic of Congo	Centre Recherche Hydrobiologie, Uvira.
Tanzania	Tanzania Fisheries Research Institute, Kigoma
	Tanzania National Parks Authority, Gombe and Mahale
Zambia	Department of Fisheries, Mpulungu

*Two members of the BLOSS team are graduates of the University of Burundi, and are currently working as secondary school teachers, but continue to be available for biodiversity survey work, through the University Biology Department.

All institutions, to a greater or lesser extent, operated under conditions of inadequate government funding, geographical isolation, lack of access to scientific resources, limited number of qualified senior staff, uncertain security situation and poor infrastructure. In institutional development, it is important to distinguish between weaknesses and constraints. Weaknesses are those factors that the project expects to be able to address. Constraints are factors beyond the remit and control of the project. Lack of skills relevant to biodiversity surveys and lack of scientific equipment are weaknesses that can, and were, addressed by BLOSS. Staff recruitment policy in government institutions, geographical isolation, and national security situations are examples of constraints beyond the capability of the project to address.

Sustainable projects are those that address weaknesses, but take account of, and attempt to function within existing constraints. Unsustainable strategies are those that use external resources and personnel to bypass local constraints temporarily. Our strategy was to identify both strengths and weaknesses in institutional capability, then build on strengths (e.g. knowledge and experience of fish taxonomy, identification, behaviour and ecology) and to address identified institutional weaknesses, such as lack of appropriate training and basic equipment. We assumed that constraints such as limited funding and low levels of senior

staff recruitment and retention would continue to operate beyond the life of the project, and designed programmes that would not require these issues to be addressed.

2.5 Biodiversity Assessment

2.5.1 Survey Design

Previous experience of biological surveys in the lake by BLOSS team members (e.g. Ntakimazi, 1995, Alin *et al.*, 1999) and some standard techniques such as gillnetting, provided initial guidance for survey design. We determined that there was a requirement for improved survey methodology that took account of both standard ecological census procedures (e.g. Sutherland, 1996) and the information requirements of biodiversity conservation planning (Jermy *et al.*, 1995; Groombridge and Jenkins, 1996).

Given the size of the task, several key decisions had to be made. We have already alluded to the need to direct survey activities towards answering conservation-related questions. This led us to choose a strategy of prioritising surveys of existing and proposed protected areas. The highest species diversity in the lake is found in the littoral and sub-littoral (Coulter, 1991; Brichard, 1989; Cohen, 1994). It is also the littoral and sub-littoral zone that is most directly impacted by land-based human activity (e.g. domestic waste disposal, sewage-pollution, soil erosion). The choice of the sub-littoral for survey activities also allowed the use of direct observation census methods using SCUBA techniques. This has two advantages: first, complex habitats and substrata can be sampled; second, survey activities can be non-destructive, thereby setting an example of biodiversity concern.

Not all areas are amenable to SCUBA survey – crocodiles, low visibility and pollution can all make SCUBA-based surveys dangerous, unpleasant and, worse still, inefficient from the sampling point of view. These areas were therefore surveyed using remote techniques: gillnetting, grab sampling and dredging.

Not all taxa can be surveyed, and it is common for biodiversity surveys to be based on small sub-sets of total diversity (see Section 2.5.2). The criteria and rationale for choice of ‘total biodiversity surrogates’ is also given in section 2.5.2.

The overall survey design adopted during the period of the BLOSS special study is indicated below. A detailed explanation of all components of the methodology is given in the BLOSS standard operating procedures (edited by Allison *et al.*, 2000, with contributions from all BLOSS team members; this document is referred to as the BLOSS SOP from now on). The methods continue to evolve, and it will be possible to add further taxonomic groups and procedures to the basic template of activities outlined in Table 2.2 (see BLOSS SOP for details).

Table 2.2 Outline of main components of biodiversity assessment surveys conducted by BLOSS survey teams between 1997 and 2000

	TARGET	TECHNIQUE	OUTPUT
PRELIMINARY	Expedition planning	Collation and assessment of large scale topographical maps	Delineation of survey area.
DIVING SAFE SCUBA TECHNIQUES CAN BE USED	Habitat	Manta Board Survey	Maps of coastal topography, land form and land use, and littoral zone (sub- and supra-) habitats to maximum depth of 10 m
		Habitat profiles: SCUBA	Fine-scale habitat map (25 m x 5m strip for each profile)
	Species	Mollusc census: SCUBA then snorkel shallows	Mollusc species or genus richness data for depths 15 - 0m
		Stationary visual fish census: SCUBA	Fish species richness, abundance and diversity index data in 10 m diameter cylinders at 15, 10 and 5 m depth
		Rapid Visual Census: SCUBA then snorkel shallows	Fish species richness data for 15 minute transects at each of four depths (15, 10, 5, 0). Likely to include patchily distributed, rarer and diver-wary species missed by stationary visual fish census, as it covers a larger area. No abundance data recorded, but relative rarity can be calculated
Multi-mesh survey gillnets set before dusk (1700) and retrieved after dawn (0800)	Fish species richness, relative abundance and diversity, to complement visual census data.		
DIVING UNSAFE DO NOT ENTER THE WATER	Habitat	Manta with crocodile box	Maps of coastal topography, land form and land use, and littoral zone (sub- and supra-) habitats to maximum depth of 10 m
		Grab samples and echo sounder	Survey of soft substrates (sand and silt)
	Species	Mollusc dredging	On hard shelves, replaces mollusc survey
		Gill nets	Day and night (as above) replaces stationary visual census.
		Grab	Survey of benthic invertebrates – planned in future

2.5.2 Choosing indicator groups or 'total biodiversity surrogates'

Biodiversity inventories are seldom, if ever, based on sampling the entire biota. Even if all biota were sampled, what attributes of that biota should be measured? Biodiversity includes the diversity of genetic composition, form and function of organisms, as well as the diversity of their interactions. Identifying the species names of all the organisms in a region is measuring just one aspect of biodiversity.

Biodiversity surveys in terrestrial systems tend to focus on vegetation types, and on groups that are well-known or easily identified, such as birds, mammals and amphibians (Jermy et al, 1995). Aquatic biodiversity surveys have tended to focus on habitat mapping (Moran et al., 1989; UNEP/AIMS, 1993), and on surveying conspicuous flora and fauna such as macroalgae (Sutherland, 1996), fish (Karr, 1981; Fausch et al; 1990; Toham and Teugels, 1999) and macroinvertebrates (Resh, 1994, Chessman, 1995).

It is important to distinguish between two separate uses of the word 'indicator' in biodiversity assessments. The traditional use of the term is in talking about taxa that are taken to be particularly sensitive or indicative of some form of perturbation, such as pollution. A more

recent usage is in talking about a sub-set of total diversity that can be used to give an indication of what differences in total (usually species) diversity might be. For example, one might use the diversity of cichlid fish as an 'indicator' for total biodiversity. For this latter use, we will use the term 'total biodiversity surrogate' (TBS) rather than 'indicator'.

Guidelines have been developed to assist the choice of suitable taxa for use as surrogate measures of total biodiversity and as indicators for impacts such as pollution and sedimentation (see SOP Section 3). The features that both indicators and total biodiversity surrogates should ideally possess are reported in Table 2.3.

Table 2.3 Features of potential total biodiversity surrogate taxa

Indicator or TBS Groups should be: <ul style="list-style-type: none">• Taxonomically well-known so that populations can be reliably identified and named;• Biologically well-understood;• Easy to survey (e.g. abundant, non-cryptic) and manipulate experimentally;• Widely distributed at higher taxonomic levels (e.g. order, family, genus) across a large geographic and habitat range;• Diverse and include many specialist taxa at lower taxonomic levels (i.e. species, subspecies) which would be sensitive to habitat change;• Representative of distribution and abundance patterns in other related and unrelated taxa;• Actually or potentially of economic importance.
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On the basis of these criteria, the groups chosen as total biodiversity surrogates for the purposes of comparative biodiversity assessments in this report are the fishes and mollusca. There is a good level of expertise in the region on fish identification, and a capability in mollusc identification has recently been developed through BIOS and LTBP training and survey activities (West and Michel, 2000). BIOS has also organised basic training and materials for identification of other invertebrate groups to higher taxon levels (Martens, 1997), and this expertise has been applied in determining the impact of sediments on invertebrates (Irvine, and Donohue, 1999; Irvine, et al, 2000), but invertebrate taxonomy and sampling methods are not yet sufficiently well known to implement in broad-scale biodiversity survey activities.

2.5.3 Habitat mapping

Much modern conservation is based on the premise that to conserve species and communities of interest, you need to sustain the habitat (biotic and abiotic processes and features) that supports these species and communities. One basic BIOS objective was therefore to ensure that all identified habitat types are represented in the existing or any proposed network of protected areas. Operational definitions of 'habitat' are given in the BIOS SOP.

Habitat characteristics and known environmental gradients determine biotic community structures. Surveys need to be stratified by the major habitat-related variables. From the practical surveying point of view, habitats therefore need to be mapped before selection of sampling localities.

Rapid, broad-scale mapping techniques in aquatic environments typically involve some form of remote sensing, such as side-scan sonar, which can differentiate hard and soft substrata. The equipment requirements are relatively modest, but nonetheless prohibitively expensive when contrasted with the operating budgets of most of the riparian institutions. Instead, a method used extensively for mapping major features of reef systems, 'manta boarding' (Moran *et al.*, 1989; UNEP/AIMS, 1993), was adopted to rapidly produce maps of areas surveyed by the present project. This method involves towing an observer, riding a plywood board and equipped with mask and snorkel, at slow speed behind a small boat. The observer notes characteristics of the substrate type. The technique is detailed in the SOP (Section 4). This is the first application of this technique in a freshwater ecosystem.

The Manta technique provided broad-scale habitat maps, covering the sub-littoral (3-10 m depth usually) at a rate of 15 km per day. The data could quickly be transcribed to maps in the field, for use as a decision tool to stratify and select sampling locations for surveys of biota (see SOP for methodology).

Within each substrate strata identified by the Manta technique, habitat-depth profiles were conducted perpendicular to the shoreline, usually from depths of 25 m up to 5 m, although this was dependent on bottom topography and slope. The habitat profiling technique was developed from adaptations of line intercept and point intercept transect methods, adapted by coral reef biologists from techniques used for botanical surveys in terrestrial environments (Kershaw, 1957; Greig-Smith, 1961; Sullivan and Chiappone, 1993; UNEP/AIMS, 1993; Rogers *et al.*, 1994). With the exception of submerged macrophyte beds, the biotic components of the habitat (substrate) are unlikely to be so strongly linked to depth in Lake Tanganyika, *within the depth range sampled*. Algal productivity in aufwuchs and episammic communities will of course be related to light intensity and therefore depth, but productivity maxima may occur at considerable depth in this clear lake (Hecky, 1991). Retrospective analysis of changes in fish and mollusc community structure by depth for each major habitat type should allow this to be differentiated.

The importance of physical habitat (principally substrate) in determining what species are found at a locality is frequently stressed in the Lake Tanganyika literature (Patterson and Makin, 1998, for review). The main concern regarding human threat, sedimentation, is based on the premise that sediments smother the rocky littoral habitats that support the highest biodiversity (Cohen *et al.*, 1993; Alin *et al.*, 1999). The methodology adopted in this study allows individual SCUBA fish and mollusc census surveys to be linked to local habitat characteristics. Although considerable detail on substrate and habitat characteristics has been collected, until large numbers of samples are analysed, or monitoring is able to detect fine-scale habitat change, linking these fine-scale features to fish and mollusc community structure will be difficult. For the purposes of this analysis, we have grouped data within very broad habitat categories, defined by depth strata and predominant substrate type (Section 2.7)

2.5.4 Survey methods for fish

Three methods of fish survey were developed, tested and deployed over the period 1997-2000: gillnet surveys, and two types of SCUBA diver surveys: stationary visual census, and rapid visual census. Detailed protocols for application of these techniques are given in the SOP (Section 5).

2.5.4.1 Gillnet surveys

Gillnet surveys were used either as the sole sampling method in areas where diving was not possible, or to complement diver-surveys. Gillnets were usually set before dusk and hauled after dawn, although some daytime gillnetting was also done, both for comparative purposes, and also where security problems and the possibility of theft prevented night-time deployment.

The gillnets used were 60m length multi-mesh monofilament survey nets, comprising twelve 5 x 1.5 m panels in mesh sizes of 8, 10, 12.5, 16.5, 18.5, 22, 25, 30, 33, 38, 45 and 50 mm half-mesh size. Nets were set parallel to the shore at a depth of approximately 10 m, during the night. Day-time sets were made at 5, 10 and 15 m. The difference was due in part to logistical reasons (gillnet surveying had to fit in with other survey activities), and in part to the observation that a set before dusk, hauled after dawn, caught fish that moved diurnally within the depth ranged sampled. A 10 m sample therefore provided an integrated catch for depth 5-15 m. Catches were recorded by number of individuals and weight per species, to provide relative abundance data for calculation of diversity indices and description of fish community structure.

2.5.4.2 Stationary visual census

Stationary visual census (SVC) provides data on the relative abundance and diversity of sub-littoral fish species. SVC data was collected in conjunction with habitat profile dives, at depths of 5, 10 and 15 m. At each depth, a 'cylinder' of the water column, to a height of 5 m above the lake bottom, and diameter 15 m (lakebed area = 177 m², volume = 884 m³) was surveyed for a 15 minute time period at each depth. Fish were identified to species and an estimate of the abundance of each species was recorded. The data allow an estimate of population density for each species to be computed. The method is developed from Bohnsack (1986), and is most suited to the survey of relatively immobile smaller species.

2.5.4.3 Rapid visual census

Rapid visual census (RVC) was also carried out at each of 5, 10 and 15 m, with some snorkel-surveys in the immediate littoral (0-1.5 m). Each RVC consisted of a 15 minute transect parallel to the shore, conducted by a pair of divers. The transect is divided into five 3-minute intervals, and the time-interval in which each species was first seen is recorded. A species seen in the first time-interval is given a score of '5', those seen in the second time-interval are given a score of '4', etc. Assuming that the more abundant species will tend to be seen soonest, the scores, when averaged across transects, can give an indication of relative abundance (although this has not been analysed for this report). The method is modified from Jones and Thompson (1978), and is intended to cover a wider area than is possible with the SVC, thus recording more mobile or less abundant species, including larger fishes.

2.5.5 Mollusc census methods

Survey for molluscs were done either by diver or using a naturalists' dredge where diving was not possible. Heterogeneity of habitats made quantitative, replicable methods of diver survey transects difficult to implement, and qualitative time-standardised search methods were employed instead, to give presence-absence data derived from known sampling effort.

2.5.5.1 Mollusc transects using SCUBA

Initially, searches were carried out at 25, 15, 10 and 5m, following dive profiles, but this was later changed to 15, 10, 5 and littoral (0-2 m), to fit in with the SCUBA fish census procedures. Searches were conducted for 10 minutes at each depth, and the identity of all species found recorded. Specimens were taken for on-shore identification where doubts over identity existed. Smaller species found in sandy substrates were also collected by sieving sand through 1 mm mesh drum sieves. Sieved samples were retained in plastic sample-jars for sorting on shore.

Exact search procedures carried out by each pair of divers at each depth were chosen according to substrate types encountered (Table 2.4).

Table 2.4 Procedures for sampling molluscs on diver-transects

Habitat Category	Diver 1 Tasks	Diver 2 Tasks
<i>Non Sandy</i> (all types of rock and gravel)	Search rocks/gravel for 5 minutes	<ul style="list-style-type: none"> • Search rocks/gravel for 5 minutes
<i>Mixed</i>	Search all micro habitats for 5 minutes	<ul style="list-style-type: none"> • Search all microhabitats for 2½ minutes • 1 x sieve sample from the sandy habitat during remaining 2½ minutes.
<i>Sandy</i>	Search for 5 minutes for larger molluscs	<ul style="list-style-type: none"> • 2 x sieve samples during 5 minute period
These operations were performed at each depth. The tasks were carried out on one side of a transect line for a total of 5 minutes and then repeated on the other side of the transect line. The total time spent sampling at each depth is therefore 10 minutes.		

It must be borne in mind that this was the final protocol developed from previous experience, and that some of the samples were taken with earlier, evolving methodology. There is

therefore some possibility of a lack of replicability between samples from earlier and later mollusc sample transects.

2.5.5.2 Mollusc dredge sampling

At locations where diving was not possible a 'naturalists dredge' was used to sample for molluscs. This technique could only be employed in areas where soft substrates were identified, as the dredge is ineffective and easily damaged on rocky substrates. Substrate type was first identified along a transect at the target sampling depth, using grab samples. The dredge was deployed from a boat positioned at the start of this transect and towed at slow speed along the transect for approximately 60-100 m

2.6 Metrics and measures of biodiversity

Measuring diversity presents philosophical and well as practical difficulties. Strictly, a measure of 'biodiversity' would be given not in terms of the number of different 'things' (species, habitats *etc.*), but in the total 'difference' or 'variability' (Zeide, 1997). The loose definition of biodiversity has hindered the development of widely accepted measures, and it is now acknowledged that what is measured must be tailored to the needs and circumstances of individual studies, perhaps to the detriment of wider comparative analysis (Purvis and Hector, 2000). We have adopted two of the most common approaches to 'measuring' biodiversity: diversity indices, and taxonomic (species) richness and related measures such as richness of endemic species. These are only two of many potential measures or indices of biodiversity, that include approaches aimed at the genetic, taxonomic, morphological, functional and ecosystem levels (Solbrig, 1991; Harper and Hawksworth, 1994; Gaston, 1996). Some alternative approaches, that we believe have potential utility for conservation-related work, are described in Section 2.12.

The immediate objective of the biodiversity survey data analysis is to use estimates, or measures, of biodiversity to compare the diversity of different areas. In this report, we use these estimates to compare between areas surveyed for possible inclusion, or retention, in a protected area network. The methodology, however, can be applied to any situation where a comparative approach is needed, e.g. comparing diversity of fished and un-fished beaches, sedimented or un-sedimented rocky habitats *etc.* The estimates may also be used to establish comparative estimates for similar habitat types in different parts of the lake (e.g. Gombe, Mahale, Nsumbu). Some comparison with previous surveys may also be possible for certain taxa, to examine changes in diversity over time.

Uses, biases, advantages and disadvantages of various diversity measures applied to biodiversity data are given in Magurran (1988), Solbrig (1991), Zar (1996), Colwell (1997), Mouillot and Lepretre (1999) and Southwood and Henderson (2000; Chapter 13). The methods chosen are based on review of these sources, and references therein.

2.6.1 Species richness

For surveys where data on abundance or relative abundance is NOT collected, the only summary statistics that can be produced are estimates of species richness. This is simply the number of species collected for a given level of sampling effort.

The advantages and disadvantages of species richness as a measure are given in Table 2.5.

When using species richness estimates to compare between areas, habitat categories or sampling methods, we first checked that sampling effort had been adequate. Methods for assessing the adequacy of sampling effort are given in Section 2.8.

Table 2.5 Advantages and disadvantages of species richness as a measure of biodiversity

Advantages	Disadvantages
An integral measure of several elements of biodiversity	Loss of information regarding species identity and no information on ecological structure and function
Relatively easy to survey, measure (taxonomic difficulties permitting!) and explain to non-specialists	No information on relative abundance of species
Comparable to existing data from literature and previous surveys	Comparability depends on adequate sampling effort in all cases

2.6.2 Calculating and comparing diversity indices

There are many different types of diversity index, but they all incorporate measures of both the number of taxa (e.g. species) and some measure of the number of individuals of each species in the sample. None of the indices available are ideal, and all were developed for purposes other than biodiversity assessment. Despite these reservations, it is still useful to calculate diversity indices as a summary measure, provided they are not calculated across different sampling methods, or across defined taxonomic groups. Diversity indices are also sensitive to sample size, tending to stabilise when sampling effort is adequate (Colwell, 1997) and so comparisons of diversity indices from incomplete or inadequate sampling must be avoided. Methods for assessing the adequacy of sampling effort are given in Section 2.8.

At present, the appropriate survey data to calculate diversity indices on are fish from gillnets and stationary visual census data (separately). The most common index is variously known as the Shannon, Shannon-Weaver, or Shannon-Weiner index:

$$H' = \sum_{i=1}^k p_i \log p_i$$

where k = the number of species and p_i is the proportion of the total number of individuals sampled in each of i species. \log_{10} was used in all calculations presented in this report. The Shannon-Weiner diversity index was calculated directly from the sample size (n) and frequency f of each species i :

$$H' = \frac{n \log n - \sum_{i=1}^k f_i \log f_i}{n}$$

H' is known to be an underestimate of the diversity of the sampled population, however, this bias decreases with increasing sample size.

Diversity indices are not normally distributed measurements, and cannot be compared statistically using standard parametric inferential methods. Comparisons of diversity indices between two or more different sites were made using a test similar to the well known t-test (Zar, 1996). The t value is the difference between the two calculated diversity indices divided by the standard error of the difference:

$$t = \frac{H'_1 - H'_2}{S_{H'_1 - H'_2}}$$

The standard error of the difference is the square root of the difference between the variances of each diversity index:

$$s_{H_1-H_2} = \sqrt{s_{H_1}^2 - s_{H_2}^2}$$

The variance of each diversity index is calculated from:

$$s_{H'}^2 = \frac{\sum (f_i \log f_i)^2 - (\sum f_i \log f_i)^2 / n}{n^2}$$

The appropriate degrees of freedom are calculated from:

$$v = \frac{(s_{H_1}^2 - s_{H_2}^2)^2}{\frac{(s_{H_1}^2)^2}{n_1} + \frac{(s_{H_2}^2)^2}{n_2}}$$

In all cases the null hypothesis tested is that the two diversity indices are the same, and the alternative hypothesis is that they are different. Two-tailed hypotheses, using the 95% confidence level were used unless specified otherwise. There is no multi-sample test to compare diversity indices, so multiple paired comparisons were done using t-tests, with the significance level of individual comparisons being adjusted by the Bonferroni approximation, at some risk of committing type II errors (incorrect acceptance of the null-hypothesis), which is statistically conservative (Zar, 1991). H' is insensitive to the presence of a few individuals of rare species in large samples. It is, however, sensitive to large differences in abundance. It is therefore useful to use other diversity indices to analyse whether inferred differences are consistent, or may be adversely affected by this type of bias. We also calculated Simpson's index, which measures the increase in the number of species per individual sampled:

$$D_v = \sum_{i=1}^k \frac{1}{p_i^2}$$

Both indices perform well for a variety of underlying distributions, and for small sample sizes. Recent simulation analyses have indicated that Simpson's index is least biased and Shannon-Weaver shows the smallest residual variance (Mouillot and Lepretre, 1999). All diversity index calculations and statistical comparisons were done in EXCEL spreadsheets, in order to familiarise BLOSS participants with the use and analysis of this type of data. Several software packages are now available to perform most of these calculations, and the 'EstimateS' package (Colwell, 1997) can also be used to examine the sensitivity of the indices to sample size.

2.6.3 Alpha, beta and gamma diversity, and rarity and endemism.

The diversity of samples all from the same community is usually referred to as alpha diversity. All the diversity indices and species richness measures mentioned above are estimates of alpha diversity. The difference in diversity between different areas or communities is known as beta diversity (Solbrig, 1991). The procedures for testing differences between areas, given above, are indirect measures of beta diversity. Gamma diversity measures the extent to which ecological counterparts occur as allopatric replacements throughout comparable habitat type, across a geographical transect (e.g. from north to south in the lake).

Beta and Gamma diversity become important when we begin to think about conservation strategies and the notion of complementarity when considering the design of conservation areas. We have also used the notion of complementarity when making a preliminary

assessment of the use of more than one survey technique to overcome selectivities and biases associated with all available methods (see below)

When considering relative conservation values of different areas, it would be usual to also examine available information on endemism, rarity, and metapopulation dynamics. Endemism is of less relevance in the Lake Tanganyika case, as levels of endemism are so high (>90% in all our samples). Rarity is not sufficiently well known to use as a criterion, and information on metapopulation dynamics is generally more relevant to conservation of individual species than of habitats or ecosystems. Its relevance to Lake Tanganyika may be in identifying intra-lacustrine distribution patterns that are common across taxa – only if this is demonstrated can population-level information be brought to bear in conservation planning (see Chapters 3 and 5).

2.7 Habitat categories for data analysis

Following recent trends in conservation research and management, we adopted a habitat-driven survey approach. There are likely to be large differences in species compositions and diversity between samples taken across known environmental gradients – substrate type and depth. For all comparative analyses, and for investigation of survey bias and the enumeration of minimum required sample sizes, all survey data were therefore initially dis-aggregated by depth and by substrate category.

The manta and profile habitat survey protocols (see SOP) allowed for collection of quite detailed habitat features (e.g. granulometry of sand, presence of particular small-scale features such as crevasses in bedrock substrate, etc.). At present, survey activity has not been extensive enough to produce sufficient replicate samples within habitat categories differentiated to such a fine scale. Prior to analysis, therefore, we have used manta and profile data to reclassify habitats on the basis of the dominant physical substratum.

In areas where diver-surveys were possible, we recognise five major physical substrate/habitat categories: shell beds, rock, mixed-rock, mixed-sand and sand. The profile and manta data record the percentages of these major categories. The percentages of each substrate that define the boundaries of each category are indicated in Figure 2.2.

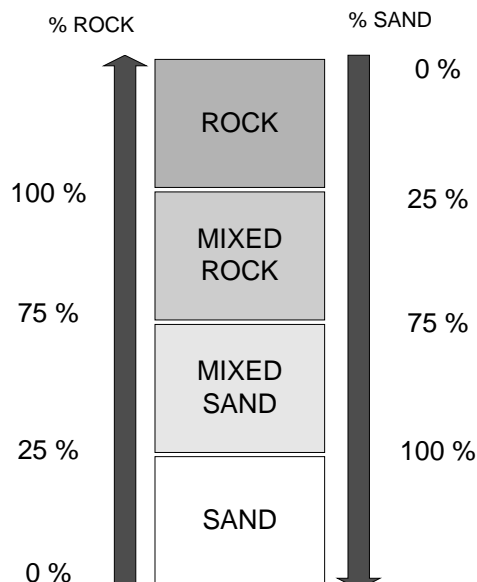


Figure 2.2 Major substrate-based habitat classifications. ‘Rock’ includes boulders, bedrock and cobbles. ‘Sand’ includes all grades of soft substratum from mud to fine gravels.

The rationale for choice of these boundaries and for this restricted range of habitats, defined purely in terms of physical substrates is as follows:

- The presence of rocks in a sand or soft substrate has a greater ecological effect than the presence of some sand in a predominantly rocky habitat.
- Mixtures of rocks, boulders, cobbles and shells effectively function as a hard substrate, and were therefore classified as either rock (if no soft substrates present) or mixed-rock. The type of rock (bedrock, boulders etc) and other features (crevices, overhangs etc) were recorded in the original profiles, but insufficient data on biota is available to investigate associations with these more detailed features of the habitat.
- All diving transects were from depths of 5m or greater, therefore habitats characteristic of the littoral fringe, such as pebble or cobble substrates and emergent macrophytes (reed beds) were not present in the main fish surveys. Some mollusc surveys and RVC fish surveys were, however, conducted in the littoral fringe. Littoral fringe substrates are accommodated within the classification scheme indicated above.
- Submerged macrophyte stands were not common in the areas surveyed, and are recorded as a secondary characteristic associated with sand and mixed-sand substrates.
- Shell beds occur overlaying soft substrates (sand, mud). Where shell beds occur, they are normally extensive, flat areas. The shells normally form dense layers, so that the substrate is normally uniform – i.e. it was usually recorded as 100% shell. There is a distinctive fish community associated with these *Neothauma* shell beds, so we have classified this as a separate habitat category.
- Analysis of frequency distributions of % substrate compositions indicated that divers tended to record these to the nearest 10% (multiples of 10 were twice as frequent as multiples of 5). It is likely that accuracy of visual estimation of substrate % cover is to within 10-20%.
- Preliminary analyses of fish-species assemblages based on these habitat classifications indicated that there were few differences in species between rock and mixed-rock substrates (Table 2.6). Very few samples fell within the mixed-sand classification. For the purposes of this report, we have therefore further reduced the above habitat categories to 3 broad littoral habitats: Rock-dominated and mixed (>10% rock), Sand-dominated (<10% rock) and shell beds. The proportion of sand/rock in the matrix may well affect community structure, but until large datasets are built up that will allow fine-scale analysis of the change in community structure associated with small differences in substrate composition, such changes will not be readily detectable.

Table 2.6 Fish species found uniquely in each of three broad substrate categories, Mahale National Park.

Rock	n	Rock (mixed)	n	Sand	n
<i>Lates mariae</i>	11	<i>Neolamprologus fasciatus</i>	5	<i>Neolamprologus tetracanthus</i>	40
<i>Gammatotria lemairei</i>	5	<i>Petrochromis macrognathus</i>	4	<i>Xenotilapia spilopterus</i>	22
<i>Simochromis babaulti</i>	5	<i>Aethiomastacembelus cunningtoni</i>	3	<i>Xenotilapia boulengeri</i>	20
<i>Julidochromis tanscriptus</i>	4	<i>Ctenochromis horei</i>	2	<i>Lamprologus ocelatus</i>	14
<i>Spathodus erythrodon</i>	4			<i>Lamprologus signatus</i>	10
<i>Julidochromis ornatus</i>	3			<i>Neolamprologus boulengeri</i>	10
<i>Acapoeta tanganicae</i>	2			<i>Neolamprologus ocellatus</i>	10
<i>Neolamprologus olivaceous</i>	1			<i>Neolamprologus wauthioni</i>	10
<i>Tropheus duboisi</i>	1			<i>Neolamprologus brevis</i>	8
				<i>Neolamprologus meeli</i>	6
				<i>Neolamprologus ornatipinnis</i>	6
				<i>Asprotilapia leptura</i>	5
				<i>Neolamprologus chrystyi</i>	5
				<i>Neolamprologus hecqui</i>	5

Rock	n	Rock (mixed)	n	Sand	n
				<i>Plecodus multidentatus</i>	5
				<i>Lamprologus ornatipinnis</i>	4
				<i>Neolamprologus leleupi</i>	4
				<i>Petrochromis trewavasae</i>	4
				<i>Petrochromis orthognathus</i>	4
				<i>Ectodus descampsi</i>	3
				<i>Neolamprologus moorii</i>	3
				<i>Aulonocranus dewindti</i>	1
				<i>Telmatochromis vittatus</i>	1

The category mixed-sand contained no species unique to that substrate. Species unique to Rock and mixed-rock are based on few individuals (n) and are likely to have arisen by chance. To increase within-category sample sizes, we pooled all 'rock' and 'mixed-rock' and all 'sand' and 'mixed-sand' substrates for subsequent analysis.

- For molluscs, the relationship between species presence and substrate characteristic is obviously very close. We therefore retained the four categories indicated in Figure 2.2, plus the shell bed category, although this resulted in the loss of some information from substrate-depth category combinations with sample sizes too small to use for further analysis.
- For areas where diving was not possible, we can only distinguish between three categories: soft and hard substrates and shell-beds. These were determined from surface inspection in shallow depths, and by grab sampling in deeper waters.
- The depth-range sampled by SCUBA was also rather narrow. Samples of fish by SVC and RVC at 5, 10 and 15m did not show consistent major differences in species composition within habitat categories (Appendix 8.2). Habitat categories were unevenly distributed with depth, despite habitat-based stratification by Manta. This is because substrates at 2-10 m (the depth range of the Manta surveys) did not often correspond with substrate characteristics in deeper waters. Some elements in the habitat-depth sampling matrix therefore consist of very few samples. To increase sample sizes for statistically valid comparisons, and given the high similarity indices between samples taken at different depths, samples were pooled across the depth range 5-15 m. This will increase within-sample variance, which in turn makes comparisons between areas statistically conservative. Pooling across depths is also justified in terms of the objectives of the study – there is no possibility in protecting areas of certain depth and not others, so there is no need to establish fine-scale depth differences for the purposes of this study, although they may be ecologically interesting.

2.8 Determining required sample sizes

In order to compare richness and diversity of fish or molluscs between sites, we need to know if our sampling effort was sufficient to include the majority of species (or at least a known proportion for the likely total diversity). In either case, we are able to use species-accumulation curves to 'correct' for differences in sampling adequacy. We will therefore be able to distinguish true differences in richness from under sampling-induced bias.

Before samples were compared to assess relative diversity of different areas, or across habitat gradients, we determined whether sample sizes within each sub-set of data were adequate. Graphical plots of cumulative species encountered against cumulative sample area will reach an asymptote when all available species in that area/habitat (that are susceptible to the survey method) have been sampled. While these plots provide a useful preliminary impression, their form may be greatly affected by the order in which the samples are added to the cumulative curve. To get round this difficulty, we plotted species accumulation curves based on 100 randomisations, using the 'Estimates 5.0' software (Colwell, 1997).

Visual inspection of 'smoothed' species accumulation curves provides a useful first impression of whether or not sampling has been adequate, but further analysis is also possible. We have fitted asymptotic models to the species accumulation curves generated by

100 randomisations of the observed species-abundance data for each set of samples. These models are used to:

- (1) measure within-inventory efficacy and completeness;
- (2) obtain estimates of species richness that are based on a standardized measure of sampling effort (making possible valid comparisons between areas sampled to a different extent - see Chapter 4) and
- (3) provide estimates for the minimum sampling effort required to reach a satisfactory level of census completeness (Moreno and Halffter, 2000).

For each of the sampling techniques used (SVC, RVC, gillnetting, mollusc transects, mollusc dredging), we generated species accumulation curves using 'Estimates 5.0'. We then used the non-linear regression module in the statistical package SPSS (v 9.0) to fit two asymptotic models to the data.

The linear dependence model is based on the assumption that the number of species collected decreases linearly as sampling effort increases:

$$S_n = a/b[1 - \exp(-bn)];$$

where n is a measure of sampling effort (for SVC, number of stationary census 'events';, for RVC, number of 15 minute transects; for gillnets, number of gillnet sets; for mollusc transects, number of searching events), S_n is the predicted number of species in the n^{th} sample, and a and b are fitted regression constants (Colwell and Coddington, 1994). The number of samples required to include a given proportion (q) of the species in the vicinity liable to be sampled by each technique is given by:

$$n_q = -1/b \ln(1 - q) \quad (\text{Moreno and Halffter, 2000}).$$

We set q as 0.9, considering sampling effort that censused 90% of the extant fauna to be adequate (theoretically, infinite effort would be required to guarantee all species were sampled).

The Clench model (e.g. Moreno and Halffter, 2000) assumes that the probability of adding species to the list decreases with the number of species already recorded, but increases over time:

$$S_n = an/(1 + bn)$$

For the Clench model, the number of samples required to include a given proportion (q) of the species is given by:

$$n_q = q/[b(1 - q)] \quad (\text{Moreno and Halffter, 2000}).$$

For both the linear dependence and Clench models S_{max} , the predicted species richness with infinite sampling effort, is given by a/b . These two models are likely to predict the upper and lower bounds of the likely true species richness of a site. The estimates of minimum sampling effort required to sample a predetermined proportion of total species present are therefore also likely to represent upper and lower bounds of estimates. The model parameter estimates and goodness of fit statistics are given in Appendix 8.3: Table 8.3, Table 8.4, Table 8.5 and Table 8.6.

2.8.1 Sampling effort for fish stationary visual census (SVC)

For the SVC, the basic unit of sampling is a single cylinder of 15 m diameter and 5 m height above the substrate, surveyed for 15 minutes. Sampling effort was expressed in terms of accumulated sampling events. This can readily be translated into area or volume sampled. Separate analyses were done for each geographical area, with samples from Sand/ mixed-

sand, rock /mixed-rock and shell-bed substrates done separately within each area. There are some samples where data on substrate composition is not available due to the mismatch between the profile dives for habitat characterisation and the fish survey activities. This was generally where depth profiles were of shallow gradient, so that divers starting a profile at 20 or 25 m did not reach the 5 or 10 m sample stations for the stationary visual fish census. This means that some samples were excluded from calculations of optimal sampling size and species richness and diversity for each substrate type. The data from these excluded samples is, however, included in generating total species lists for each sampled area and comparing total recorded species for conservation prioritisation purposes (Chapter 5).

The SVC technique was not used much in Burundi, and sample sizes did not provide adequate basis for estimating total species richness, nor even for determining which model of sample species accumulation curve is more appropriate (Figure 2.3). Three or four sample dives per locality/substrate combination is clearly inadequate, yet is fairly typical of previous diver-surveys used to compare species richness between areas (e.g. Alin et al, 1999). The rocky habitats of the Pemba, Luhanga, Bangwe area and the sandy habitats in the vicinity of Uvira (both in the DR of Congo) were more intensively sampled using this technique, and show a clearly asymptotic pattern (Figure 2.3). Asymptotic models predicting the effects of additional sampling can therefore be fitted with greater confidence.

Although more than 15 diver SVC surveys of fish were undertaken on both rocky and sandy sites at Gombe, species accumulation curves had not yet levelled off, implying greater sampling effort would be needed (Figure 2.4). For the very diverse rocky areas of Mahale, continued slow increase in species is seen, even though more than 25 SVC surveys were undertaken. In the case of both sandy and rocky substrates in Mahale, the Clench model, which predicts a continued slow increase in species sampled as sample size increases, appears to provide the most realistic fit (Figure 2.4). There are no statistical criteria for separating the fit of the Clench and Linear dependence models ($r^2 > 0.99$ in most cases – see Appendix 8.3, Table 8.3) but that is mostly because much of the data are from the steep part of the species-accumulation curve, where both models provide a similar fit. It is in their behaviour in reaching an asymptote that the two models reveal a crucial difference. This difference has considerable ramifications for predictions of 'true' species richness, and of the minimum sampling size required to estimate an acceptable proportion (90% is chosen in this study) of that richness.

The SVC technique was also used only occasionally in Zambia, where many sites cannot be dived because of the risk posed by crocodiles. Only for the rocky sites in the Katoto area were sample sizes sufficiently large to estimate species richness and minimum required sampling size with any confidence (Figure 2.5).

Table 2.7 indicates that some areas were adequately sampled (>90% of estimated total species present in the areas sampled), while other areas were under sampled. It is clearly seen that it is difficult to recommend a single minimum required sampling size, as this varies with location and substrate.

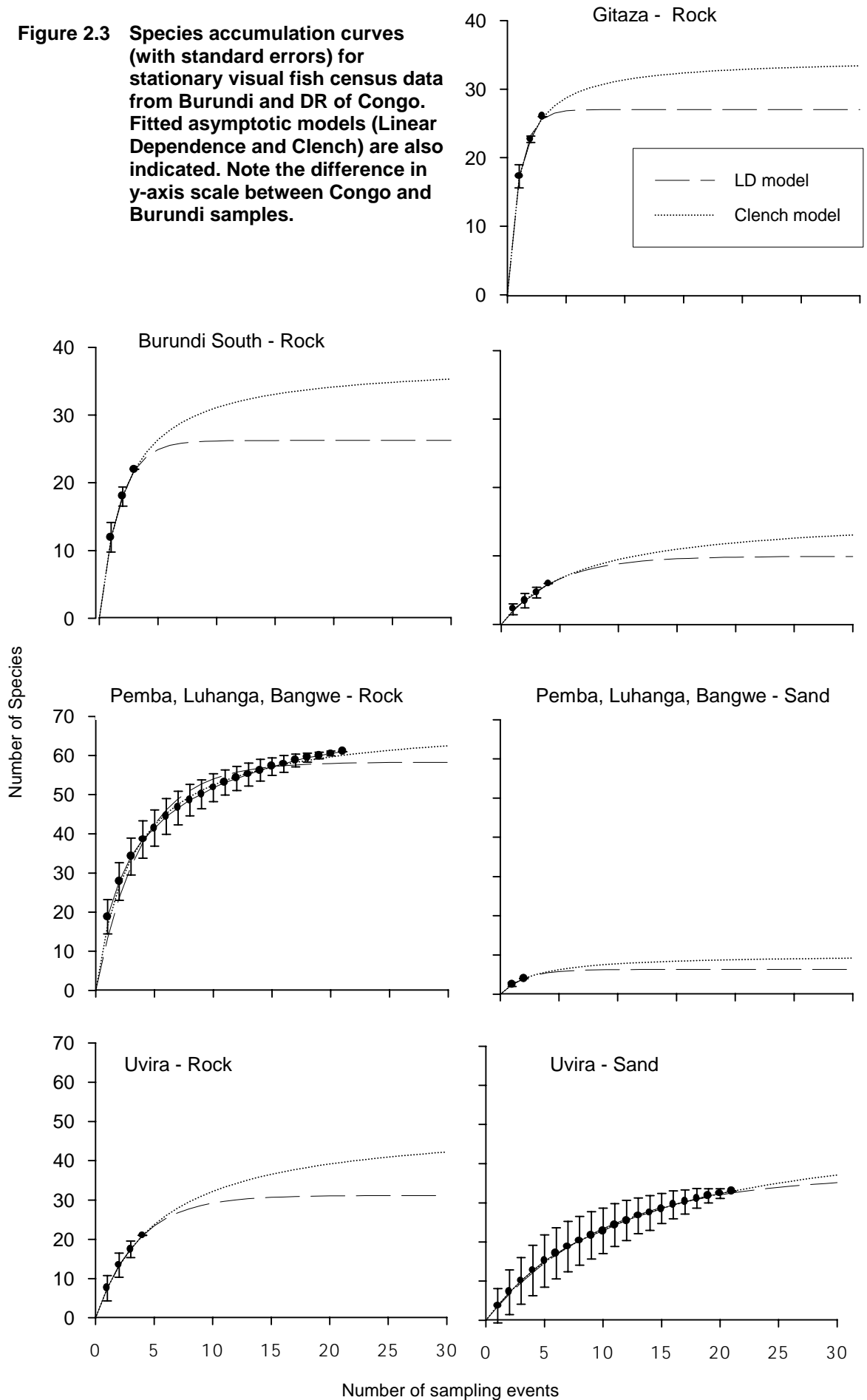
In general, sandy substrates require equal or greater sampling effort to rocky and mixed habitats in the same areas. This may seem surprising at first, given that they have generally lower species richness. However the sand-dwelling species are more mobile, and often schooling. This means that probabilities that additional samples will yield additional species can be high.

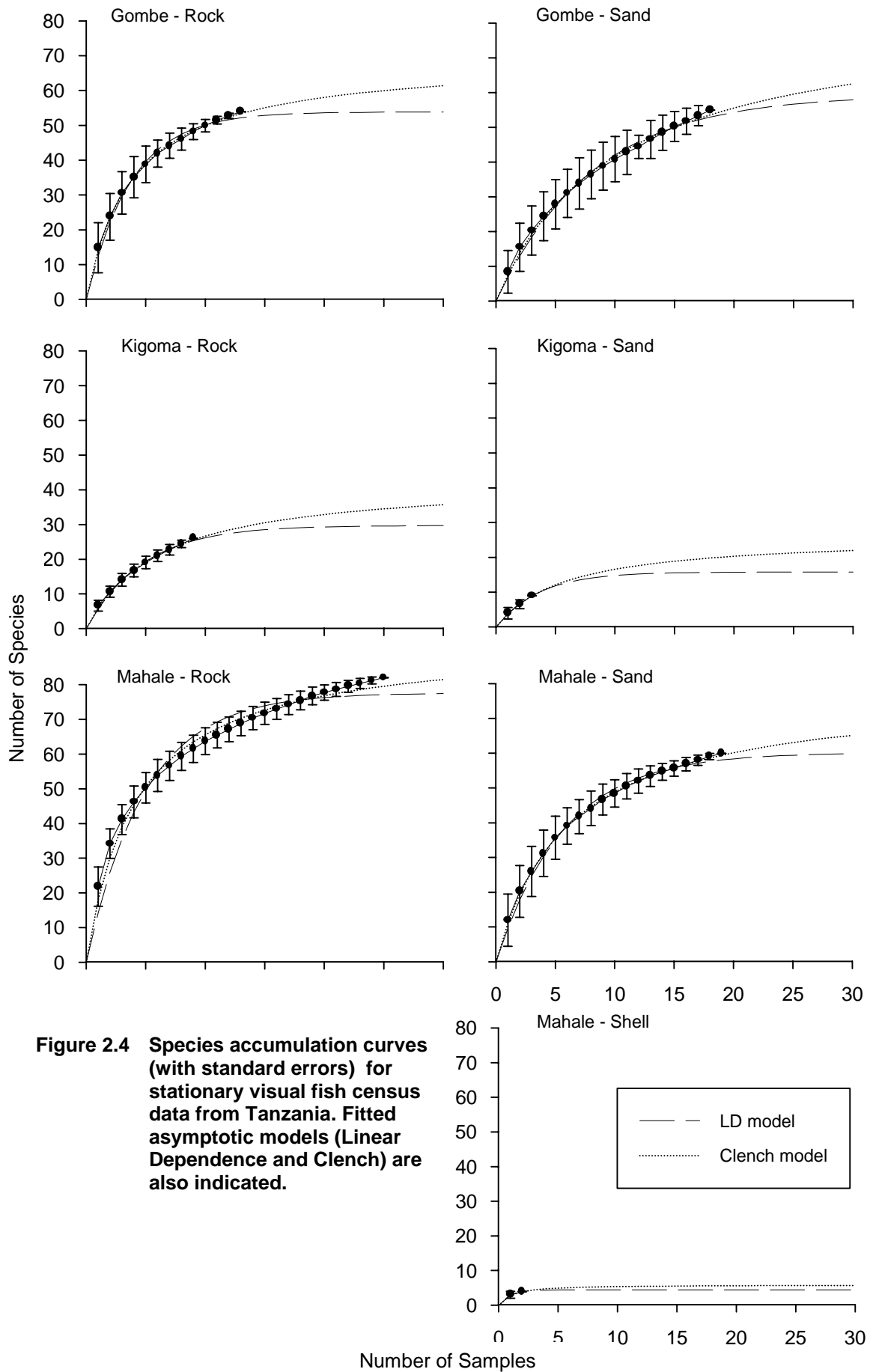
The two asymptotic models used to extrapolate 'true' species richness from partially sampled populations perhaps represent upper and lower bounds of these estimates. Minimum required sampling sizes estimated from the linear dependence model vary from 2 to 20 samples (mean = 9), while estimates from the Clench model vary from 9 to 120 (mean = 47).

The linear dependence model suggests that, while Mahale, Gombe, Gitaza and some of the sites in DR of Congo were adequately sampled, other areas dived in Burundi and Zambia were under sampled, as were the sandy areas at Pemba, Luhanga, Bangwe, and rocky areas at Uvira (DR of Congo). The Clench model seems to predict very high species richness and

therefore suggests that insufficient replicate samples were taken with the SVC technique at all sites. The predictions of the Clench model are not strongly supported by comparison of our sampling with the total recorded species in the lake (Table 5.5). BLOSS surveys have, in aggregate, sampled over 80% of recorded lacustrine fish species. This suggests that the Clench model overestimates species richness and overestimates the number of samples required to census the fish populations. For the areas that were better sampled, however, the pattern of species accumulation would suggest that the Clench model may be more appropriate. Given this rather contradictory evidence, we suggest that future sampling should be based on at least 20 SVC samples per survey strata until species-accumulation curves become better known and defined.

Figure 2.3 Species accumulation curves (with standard errors) for stationary visual fish census data from Burundi and DR of Congo. Fitted asymptotic models (Linear Dependence and Clench) are also indicated. Note the difference in y-axis scale between Congo and Burundi samples.





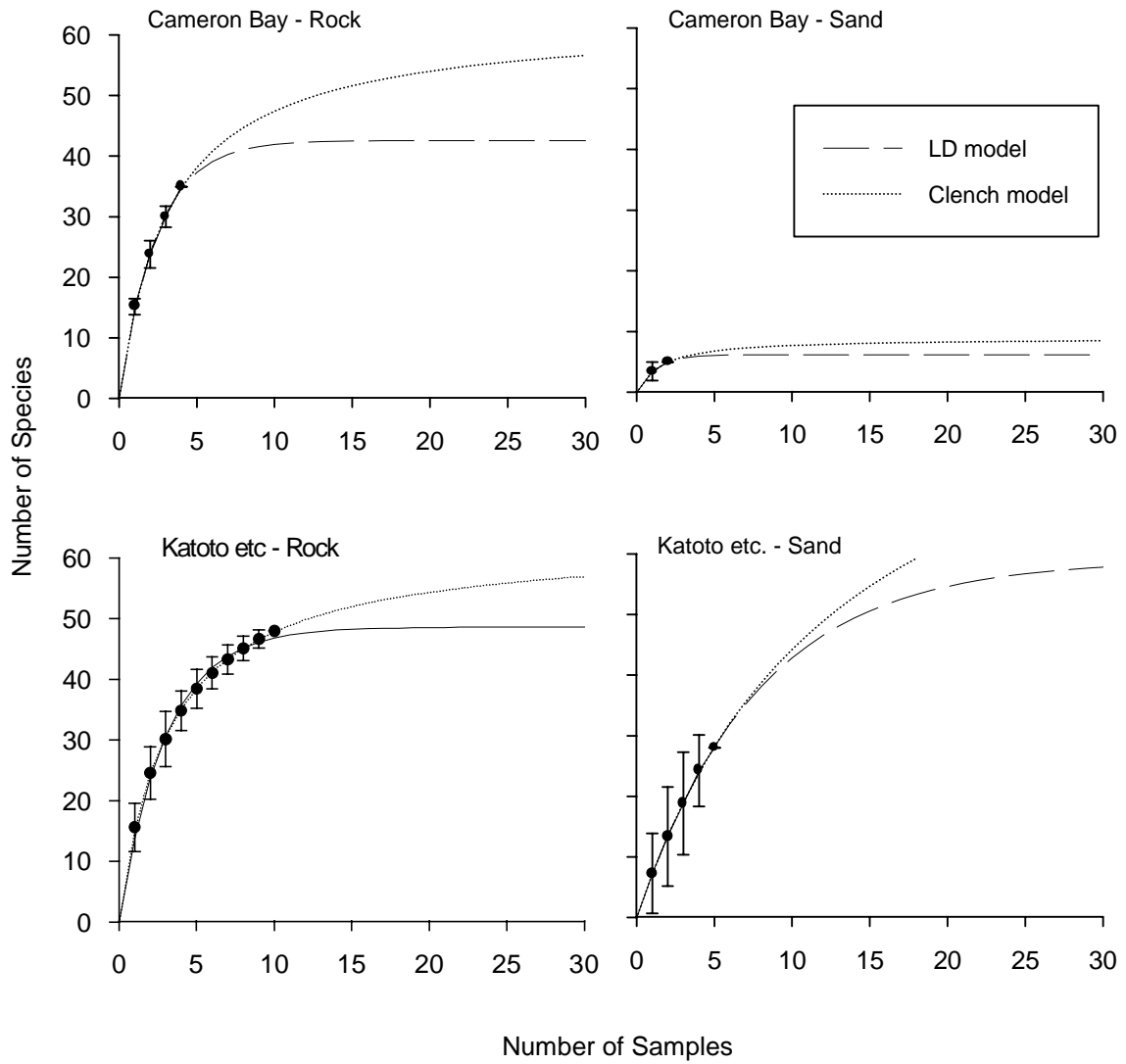


Figure 2.5 Species accumulation curves (with standard errors) for stationary visual fish census data from Zambia. Fitted asymptotic models (Linear Dependence and Clench) are also indicated

Table 2.7 Analysis of sampling adequacy for stationary visual census of fish species, using two asymptotic models (see text for details)

				Linear Dependence Model			Clench Model		
Area	Substrate	N	S _{obs}	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})
BURUNDI									
Burundi South	Rock	3	22	26	84	4	38	58	20
Burundi South	Sand	4	6	10	60	10	16	37	63
Gitaza	Rock	3	26	27	96	2	35	75	9
DR CONGO									
Pemba etc	Rock	21	61	58	105	9	69	88	28
Pemba etc	Sand	2	4	6	63	5	10	39	28
Uvira	Rock	4	21	31	67	8	50	42	50
Uvira	Sand	21	33	37	89	23	53	62	116
TANZANIA									
Gombe	Rock	13	54	54	100	9	69	78	35
Gombe	Sand	18	55	60	92	19	83	66	90
Kigoma	Rock	9	26	30	87	11	43	60	55
Kigoma	Sand	3	9	16	57	8	26	34	52
Mahale	Rock	25	82	78	106	11	93	89	37
Mahale	Sand	19	60	60	100	13	78	77	54
Mahale	Shell	2	4	4	89	2	6	68	9
ZAMBIA									
Cameron Bay	Rock	4	35	43	82	5	63	56	29
Cameron Bay	Sand	2	5	6	81	3	9	56	14
Katoto etc	Rock	10	48	49	99	7	63	76	29
Katoto etc	Sand	5	28	59	48	18	103	27	120

N = number of SVC samples, S_{obs} = observed number of species in those samples, S_{max} = estimated species richness, N_{req} = the number of samples that would be required to sample 90% of the estimated species present. Note that estimates of S_{max} and $S_{obs}:S_{max}$ are rounded to the nearest integer but that the calculations of have been made with the original un-rounded estimates.

2.8.2 Sampling effort for rapid visual census (RVC)

For the RVC, the basic unit of sampling is a single linear transect, defined in terms of time (15 minutes), rather than distance covered. Sampling effort was expressed in terms of cumulative number of sampling transects, but this could readily be converted to cumulative sampling time or estimated area if required. Samples were not grouped by substrate, as the RVC sampling frequently integrated across substrate types, so no meaningful separation could be made. This will add to the variance and tend to over-estimate the required minimum sampling effort for the area as a whole.

Because the RVC technique was applied in both the shallow sub-littoral (5-15 m) and the littoral fringe (0-3 m), whereas the SVC technique was used only for 5-15m, we analysed these two depth bands separately. Four transects were also done in the 16 to 25 m depth band as part of survey activities in Zambia, but limitations of bottom-time (and air supply) for no-stop SCUBA diving probably preclude routine surveys at this depth and beyond. This data is not included in the analysis. Species accumulation curves with fitted asymptotic models are given in Figure 2.7, Figure 2.8 and Figure 2.9.

Figure 2.7 Species accumulation curves (with standard errors) for rapid visual fish census data from Burundi. Fitted asymptotic models (Linear Dependence and Clench) are also indicated

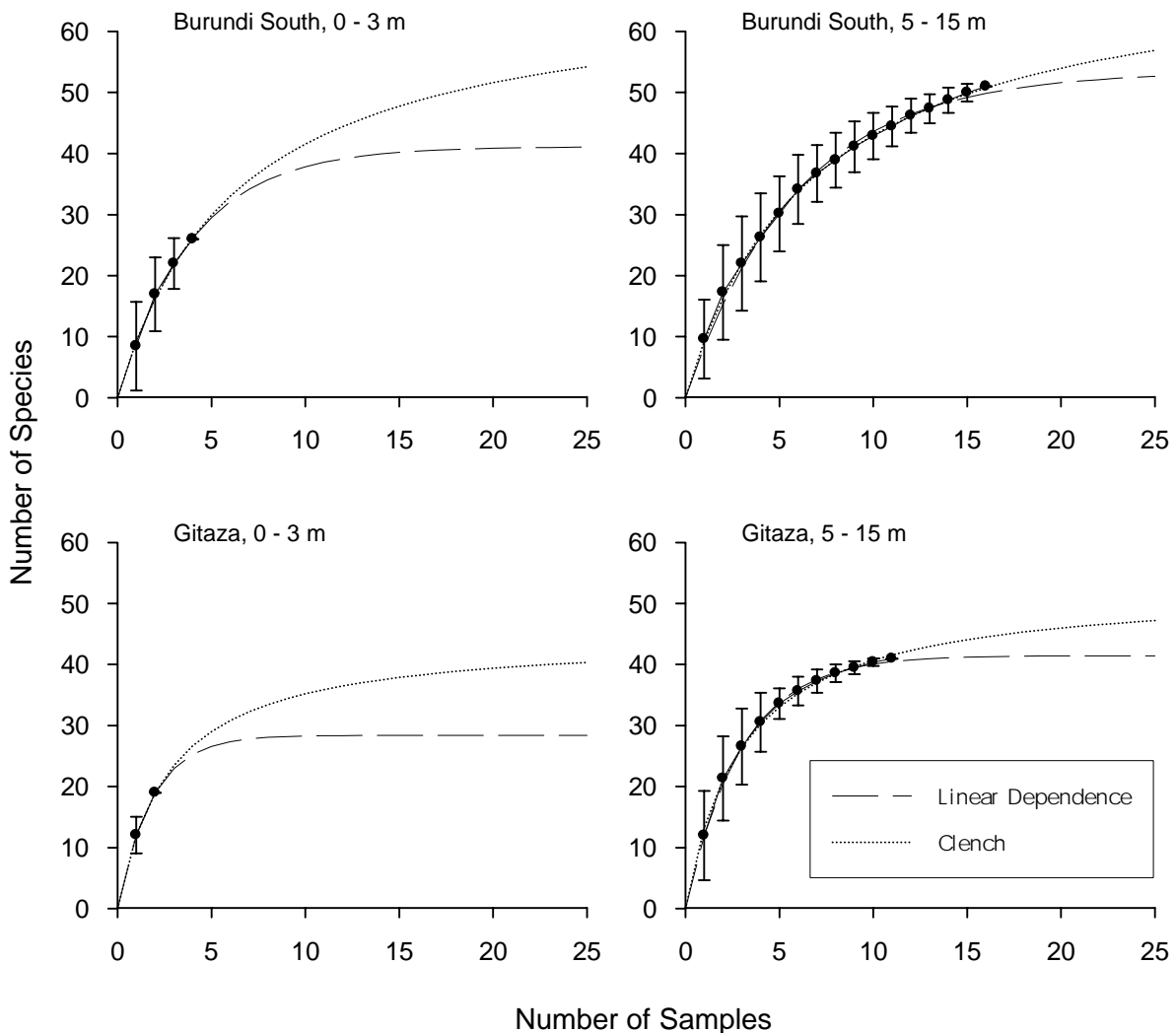


Figure 2.8 Species accumulation curves (with standard errors) for rapid visual fish census data from DR Congo and Zambia. Fitted asymptotic models (Linear Dependence and Clench) are also indicated. Note the different X and Y axis scales for DR Congo and Zambia.

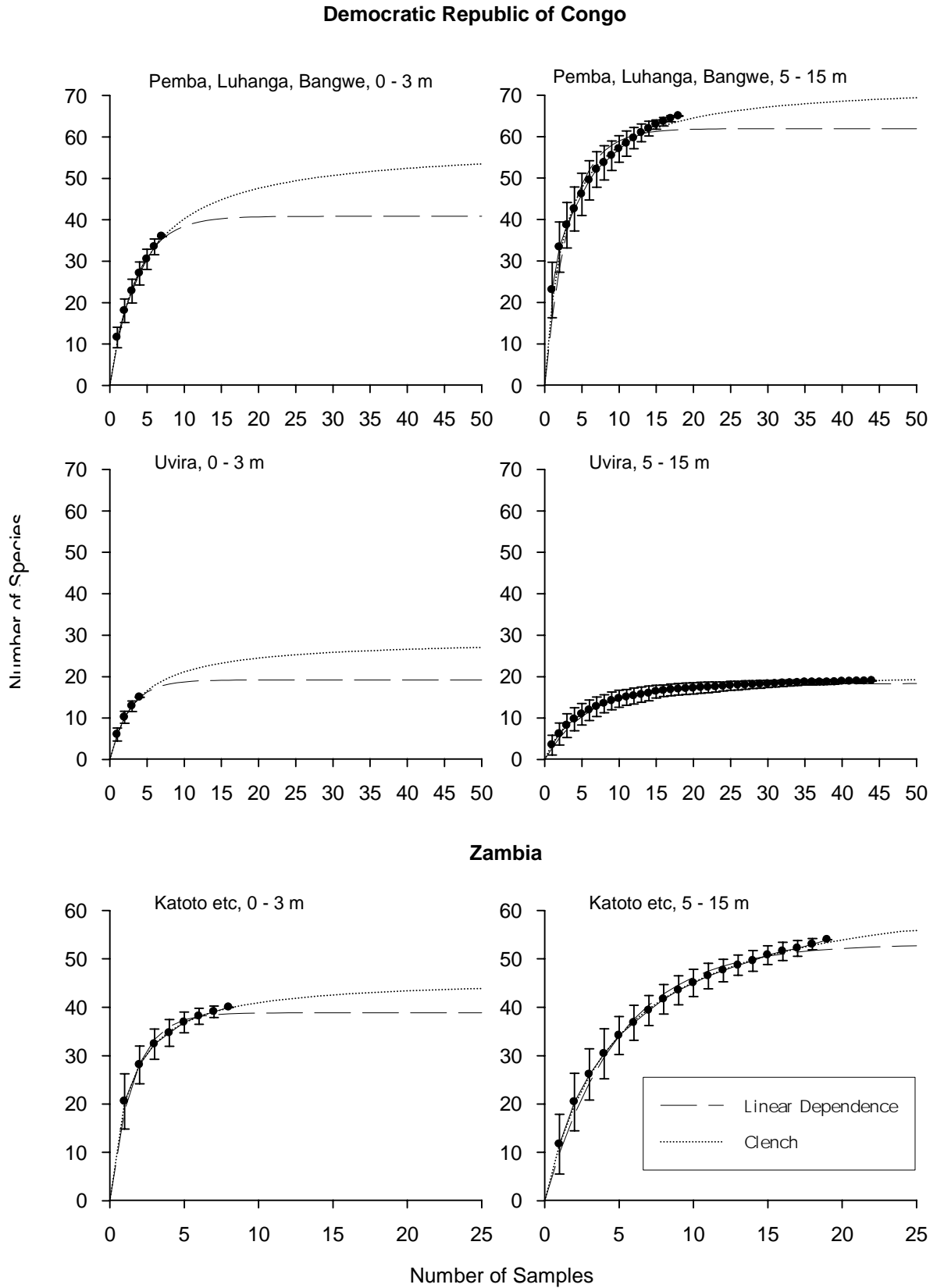


Figure 2.9 Species accumulation curves (with standard errors) for rapid visual fish census data from Tanzania. Fitted asymptotic models (Linear Dependence and Clench) are also indicated. Note the different X and Y axis scales for Mahale and Kigoma. This is done for clarity of presentation.

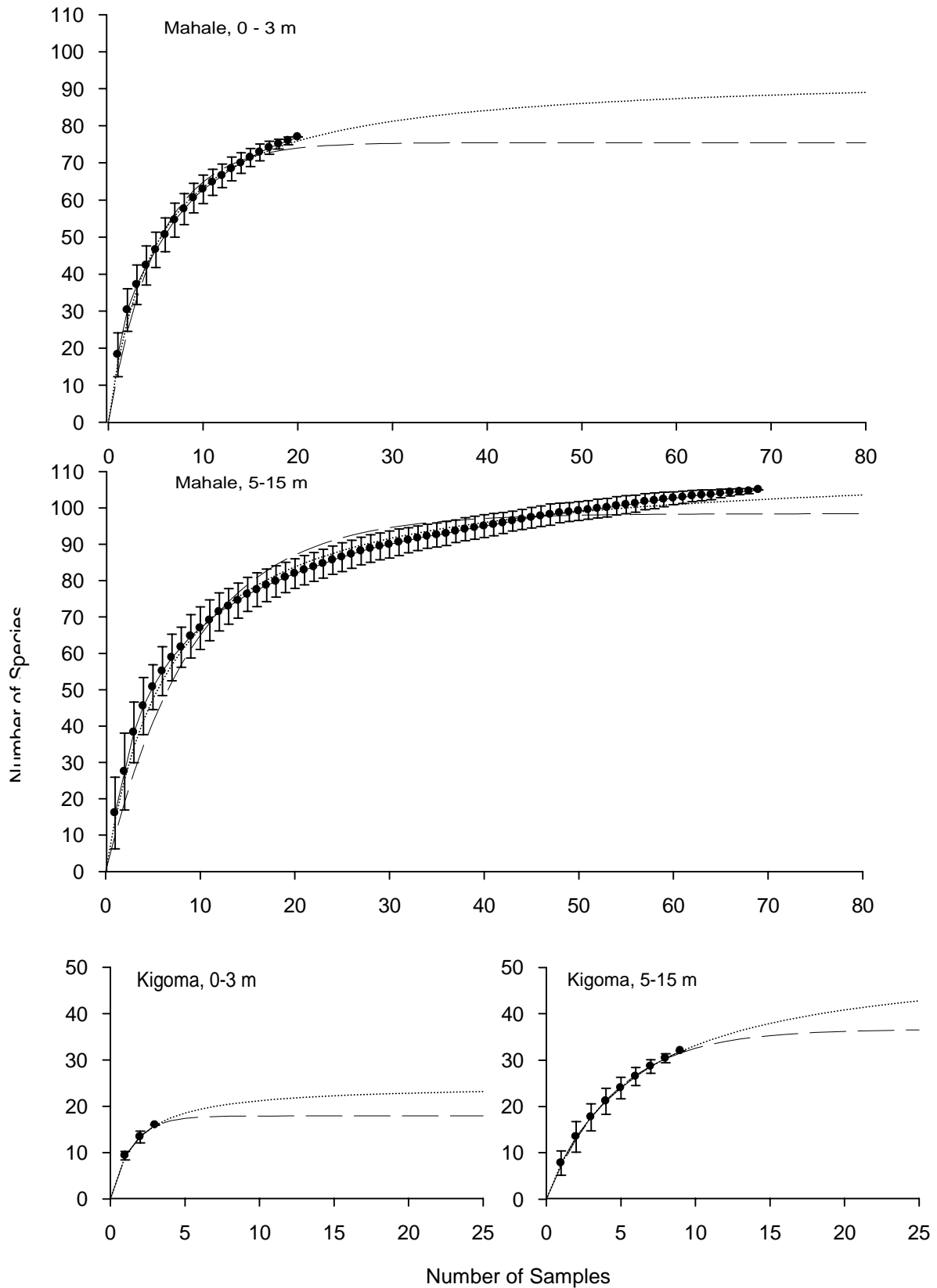


Table 2.8 Analysis of sampling adequacy for rapid visual census (RVC) of fish species, using two asymptotic models (see text for details)

				Linear Dependence Model				Clench Model	
Area	Depth range (m)	N	S _{obs}	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})
BURUNDI									
Burundi South	0 to 3	4	26	41	63	9	68	38	57
Burundi South	5 to 15	16	51	53	96	14	73	70	62
Gitaza	0 to 3	2	19	28	67	4	45	42	24
Gitaza	5 to 15	11	41	42	99	7	53	77	27
DR CONGO									
Pemba etc	0 to 3	7	36	41	88	8	58	62	40
Pemba etc	5 to 15	18	65	62	105	8	73	89	24
Uvira	0 to 3	4	15	19	78	6	29	52	34
Uvira	5 to 15	44	19	18	103	14	21	90	41
TANZANIA									
Kigoma	0 to 3	3	16	18	89	3	25	65	15
Kigoma	5 to 15	9	32	37	87	11	53	60	54
Mahale	0 to 3	20	77	75	102	12	94	82	44
Mahale	5 to 15	69	105	98	107	21	113	93	62
ZAMBIA									
Katoto etc	0 to 3	8	40	39	103	4	46	87	11
Katoto etc	5 to 15	19	54	53	102	11	67	81	43

N = number of RVC samples, S_{obs} = observed number of species in those samples, S_{max} = estimated species richness, N_{req} = the number of samples that would be required to sample 90% of the estimated species present. Note that estimates of S_{max} and S_{obs}:S_{max} are rounded to the nearest integer but that the calculations of have been made with the original un-rounded estimates.

Although RVC data from the 5-15 m depth band Burundi South and Gitaza were sufficient to identify a reasonably narrow range for the likely total species richness, under sampling at the 0-3 m depth band means that extrapolations are rather unreliable (Figure 2.7), thus leading to unreliable estimates of minimum required sample sizes (Table 2.8) and difficulty in determining which asymptotic model provides the best fit to the randomised species-accumulation curve.

Examination of the better-sampled areas in samples from the DR of Congo and Zambia (Figure 2.8) indicates that the Clench model may provide the best fit to the observed species-accumulation curves for the Rapid Visual Census technique as well. This is confirmed by examination of the species-accumulation curves from Mahale (Figure 2.9), where the Clench model provides a better fit even in the steeper part of the species accumulation curve.

RVC surveys (Table 2.8) generally recorded slightly higher species numbers than SVC surveys (Table 2.7) probably because they covered larger areas and included larger and more mobile species, but perhaps at the expense of smaller, cryptic species. According to the Linear Dependence model, an average of 9 RVCs are usually adequate to sample 90% of estimated total species present (Table 2.8), sometimes fewer, depending on richness and patchiness of the survey area. According to this model, most areas were sampled adequately by the BLOSS team. Once again, the Clench model estimates much higher required sample sizes (11-62, averaging 38). If this model is accepted, then only Pemba, Bangwe and Luhanga, Uvira and Mahale were adequately sampled for the depth range 5-15m. By pooling samples taken at 5, 10 and 15 m we increased sample size but probably also increased variance. For the 0-3 m snorkel-based RVCs, sampling sizes were smaller (generally one snorkel survey for each 3 dive surveys at 5-15m). Future surveys should aim to carry out at least 10 RVCs per survey strata, and, if the Clench model is more accurate, 40 RVC transects would be more likely to ensure that an adequate proportion (90%) of the fish species present were recorded. Once again, this number will vary with species richness and habitat heterogeneity, and will therefore be difficult to fix in advance.

2.8.3 Sampling effort for gillnetting

For gillnet samples, it was not always possible to standardise setting time, as gillnetting was often conducted alongside other survey activities. In theory, one could correct for differences in sampling time assuming that gillnets set for longer caught more fish (and therefore were likely to sample more species). The assumption is that there is a linear relationship between the time the gillnet is in the water and what it catches. This assumption may not be valid (Minns and Hurley, 1988), so we have tested it using data from gillnets set overnight in Mahale: times in the water varied due to survey logistics, but showed no significant relationship with catches (Figure 2.10).

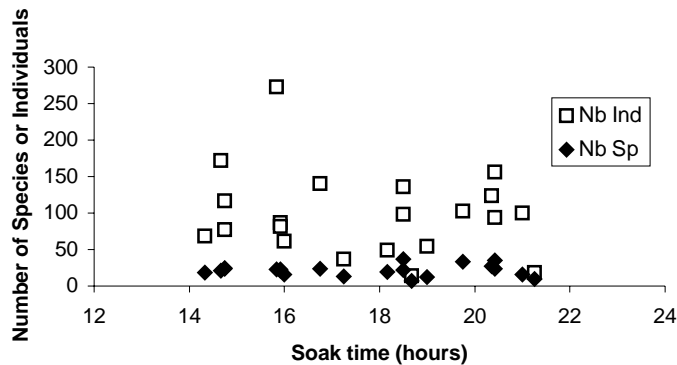


Figure 2.10 Scatter plot of soak times against the number of species and individuals caught in gillnets set overnight within Mahale National Park, based on 21 sets.

There is no significant (linear) relationship between set time and total catch ($r^2 = 0.04$, $F = 0.764$, $P_{1,19} = 0.39$) or set time and number of species sampled ($r^2 < 0.001$, $F = 0.01$, $P_{1,19} = 0.91$) so we assume that the shortest time of setting (14 hours) exceeds the 'saturation time' for the net, and treat each set as being equivalent replicate samples.

For Rusizi, nets were set consistently at 1700 and hauled at 0800 (15 hours). Mahale net sets can be treated as equivalent sampling units, as can nets set in other locations, which covered similar time periods. Daytime gillnet sets in Rusizi were always done for the same time (0900 – 1500; 6 hours), so no test of the effects on soak time against catch could be performed. The shorter time that nets set in the daytime were fished for may account, at least in part, for their lower catches, in terms of both species and individuals. The minimum ideal sampling time for adequate representation is thus yet to be determined.

Having ascertained that catches were not closely related to soak times, we use a 'gill net set' as our standard sampling unit. Attempts were made to standardise the setting times as 15 hrs overnight and six hours during the day for surveys conducted elsewhere. These units of sampling effort are obviously applicable only to the net configurations used in our programme, and future surveys using different gear should recalibrate minimum sampling effort required.

We plotted species accumulation curves in order to assess the number of replicate sets of gillnets needed to sample all fish vulnerable to gillnetting in an area. Separate analyses were done for gillnets set during the day, and overnight, using data from surveys conducted along the Burundi, Congo, Tanzanian and Zambian coast.

This analysis addresses the question: how much gillnetting effort is needed to sample the fish community adequately, and does this differ between night and day, or between areas (as a function of patchiness and/or diversity)? This can be answered by finding out how much cumulative effort is needed before no new species are found in successive gillnet samples. The number of species caught in each set is recorded, and the cumulative species calculated by checking the number of new species added by each successive net set. Each sub-set of data was selected, and successive individual net sets were added to the data-set at random. One hundred such randomisations were performed, using the Estimates 5 Software (Colwell, 1997).

The data come from a mixture of planned, intensive surveys of particular areas (e.g. Uvira, Rusizi, Mahale, Nsumbu) and more opportunistic and sporadic deployment during training and exploratory surveys. The latter tend to suffer from under sampling (see individual graphs in Figure 2.11, Figure 2.12, Figure 2.13).

Quite large gillnet samples were taken in the northern part of the Lake (Burundi and DR Congo), even with limitations on night-time gillnetting imposed by the security situation. Day/night comparison based on similar sample sizes is possible in Rusizi, where it is clear that night-time netting gives higher estimates of species richness (Figure 2.11). Even for well-sampled areas, the curves have not reached a clear asymptote. Instead, the Clench model, with its continued gradual rise in estimated species richness, seems to fit the data best. This implies that there are relatively large numbers of rare or infrequently encountered species, and good estimates of total richness can only be made with very large sample sizes. This is well illustrated for Mahale (Figure 2.12), where after 23 gillnet sets the species accumulation curve had still not reached an asymptote.

Gillnetting was an important sampling method in Zambia, where diving opportunities are severely constrained by threats from crocodile and hippo attack. Although a good range of areas were sampled in Zambia, the low sample size leads to uncertainty over predicted asymptotic species richness (Figure 2.13). It is clearly seen that the shorter the observed species-accumulation curve, the greater divergence there is between predicted species richness extrapolations from the two asymptotic models. This further illustrates that extrapolation tools, while they can be useful to gain preliminary estimates of species richness, are no substitute for a well-replicated sampling programme.

Figure 2.11 Species accumulation curves (with standard errors) for gillnet survey in Burundi and DR Congo waters. Fitted asymptotic models (Linear Dependence and Clench) are indicated.

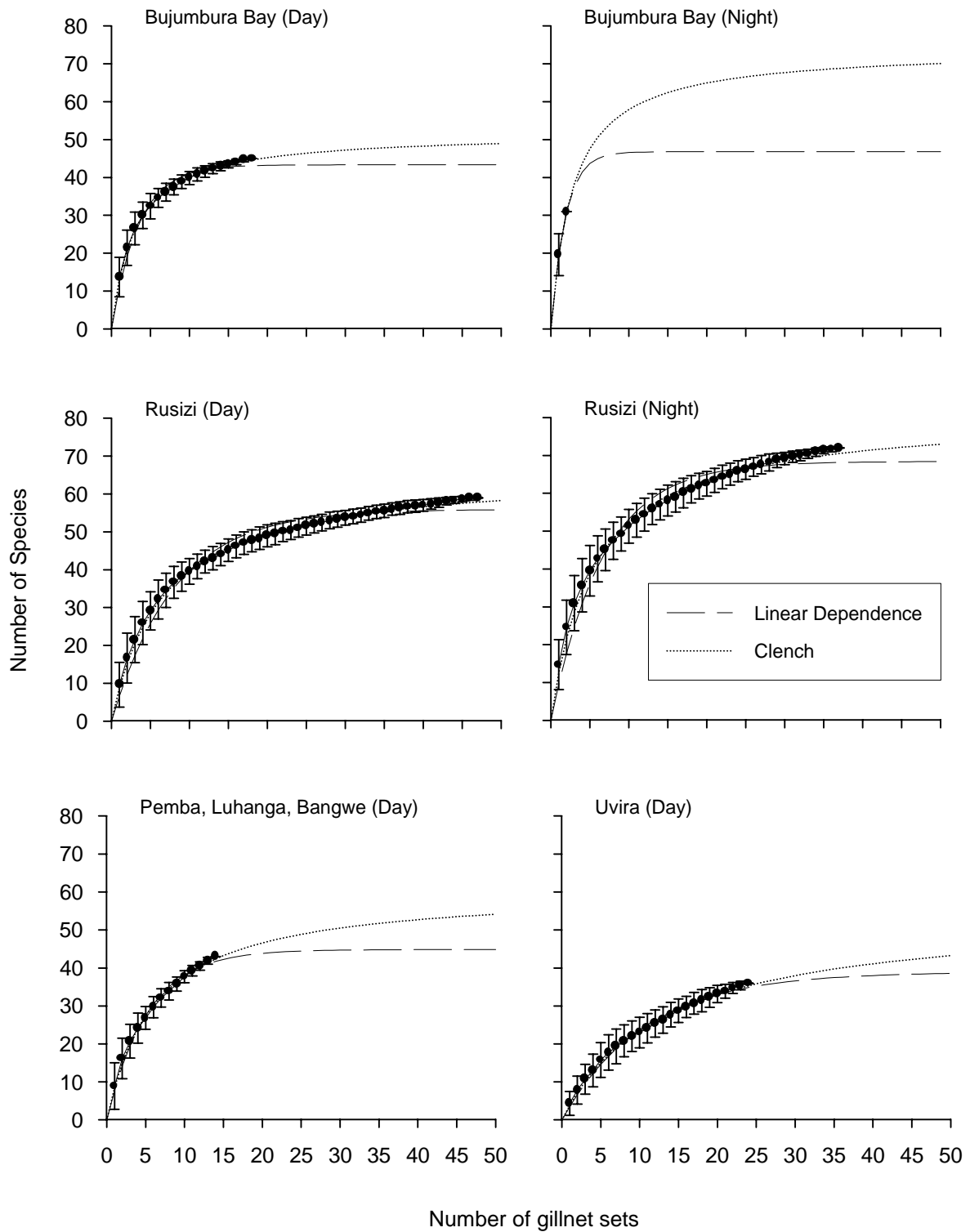


Figure 2.12 Species accumulation curves (with standard errors) for gillnet survey in Mahale National Park, Tanzania. Fitted asymptotic models (Linear Dependence and Clench) are indicated.

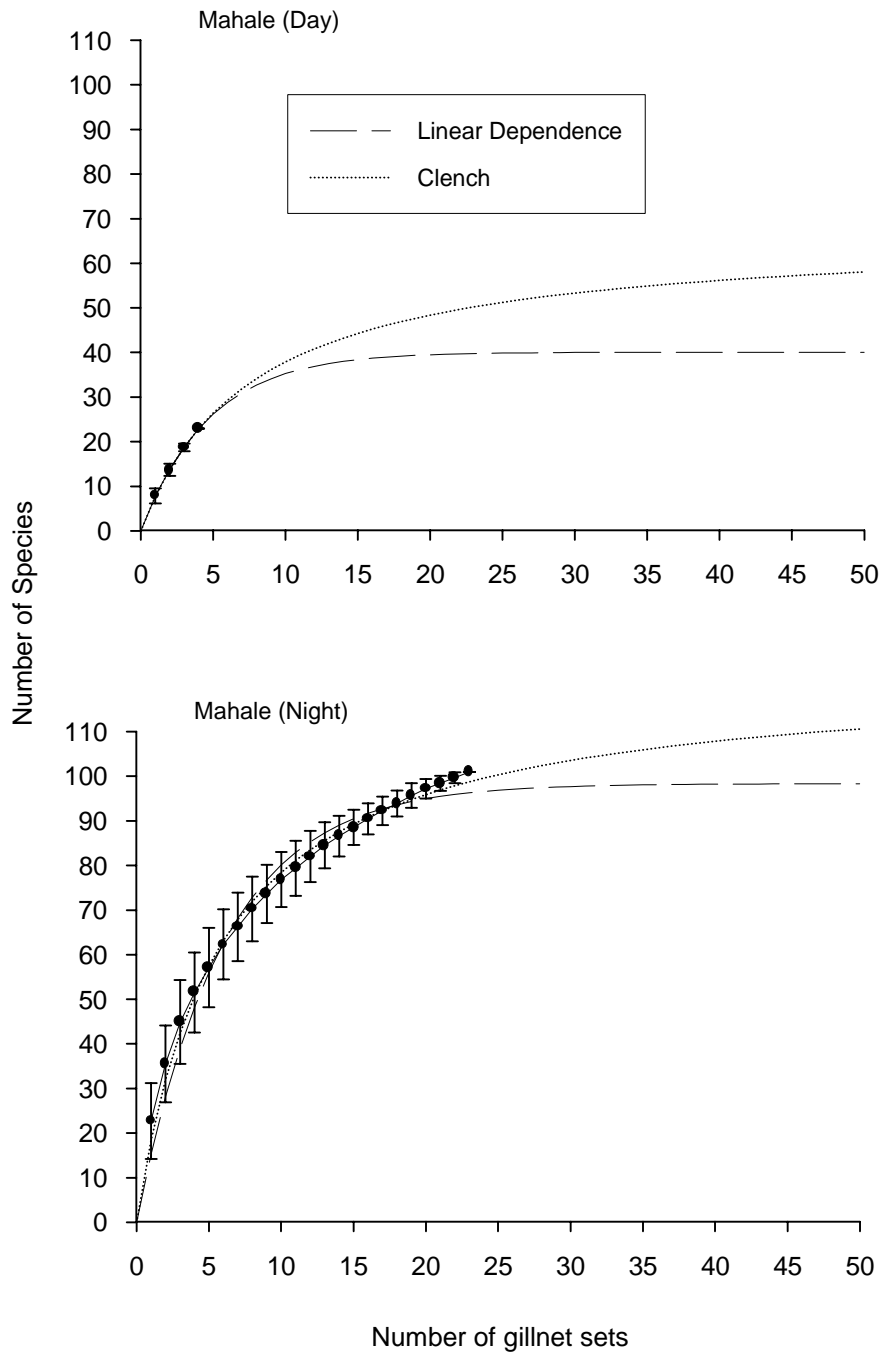


Figure 2.13 Species accumulation curves (with standard errors) for gillnet surveys in Zambian waters. Fitted asymptotic models (Linear Dependence and Clench) are indicated. Note the Y-axis for the Lufubu sample is on a different scale to the rest (0-110 species, instead of 0-90)

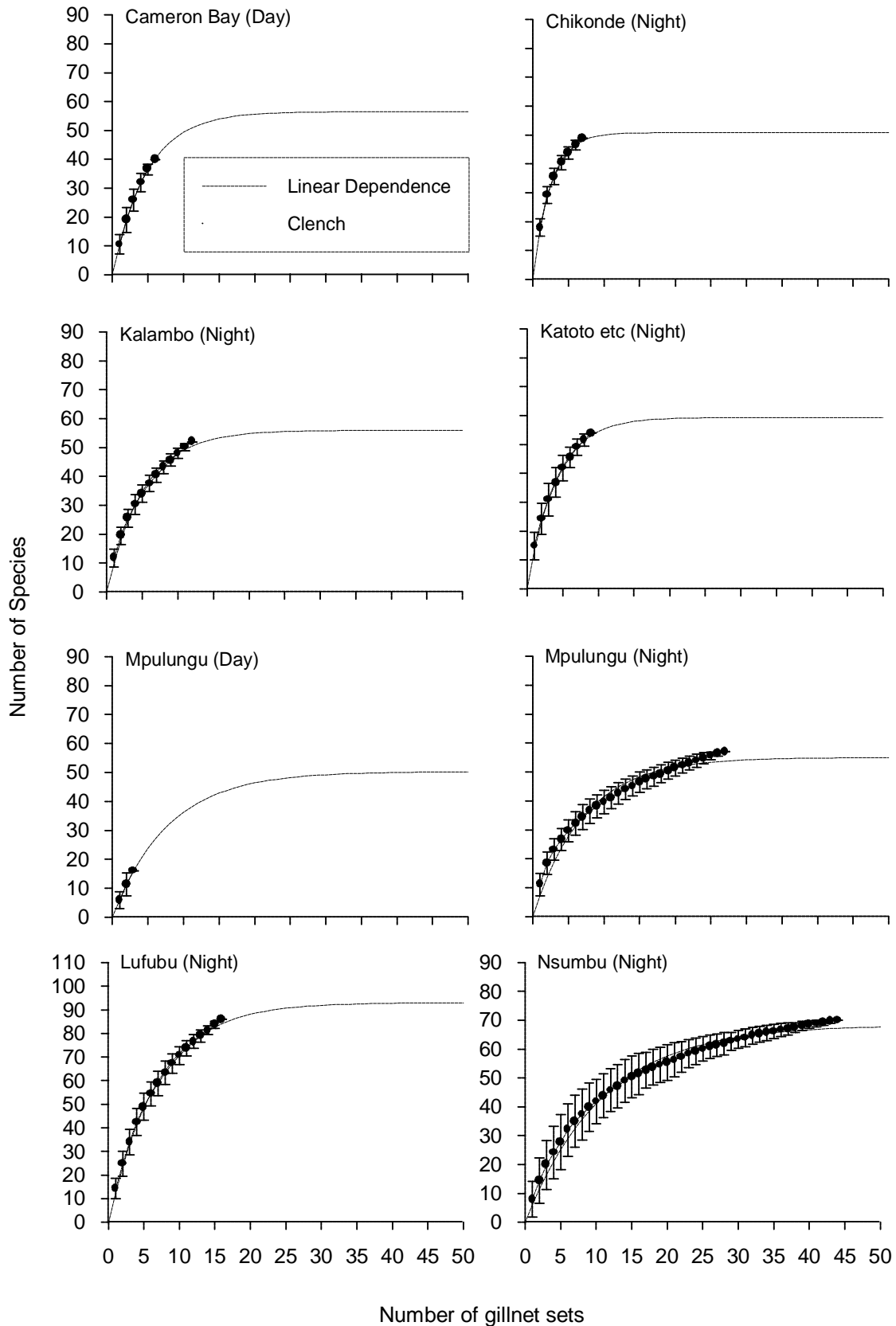


Table 2.9 Analysis of sampling adequacy for gill net sampling of fish species, using two asymptotic models (see text for details).

				Linear Dependence Model			Clench Model		
Area	Set-time	N	S _{obs}	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})
BURUNDI									
Bujumbura Bay	Day	18	45	43	104	8	52	87	26
Bujumbura Bay	Night	2	31	47	66	4	74	42	25
Rusizi	Day	47	59	56	106	19	66	89	60
Rusizi	Night	37	72	69	105	15	81	89	49
DR CONGO									
Pemba, Luhanga, Bangwe	Day	14	43	45	96	12	61	71	55
Uvira	Day	24	36	39	92	24	55	66	118
TANZANIA									
Mahale	Day	4	23	40	58	11	67	34	69
Mahale	Night	23	101	98	103	14	132	77	51
ZAMBIA									
Cameron Bay	Day	6	40	57	70	11	90	58	66
Chikonde	Night	7	49	51	96	6	68	72	24
Kalambo	Night	12	52	56	93	12	78	67	56
Katoto etc	Night	9	54	59	92	9	83	65	44
Lufubu	Night	16	86	93	92	16	130	66	76
Mpulungu	Day	3	16	50	32	18	92	17	129
Mpulungu	Night	27	57	55	104	16	69	82	62
Nsumbu NP	Night	44	70	69	102	25	86	81	95

N = number of gillnet samples, S_{obs} = observed number of species in those samples, S_{max} = estimated species richness, N_{req} = the number of samples that would be required to sample 90% of the estimated species present. Note that estimates of S_{max} and S_{obs}:S_{max} are rounded to the nearest integer but that the calculations of have been made with the original un-rounded estimates.

N.B. The daytime set at Katoto etc is excluded (N = 2) as both fitted models failed to reach an asymptote.

Estimates of sampling size required to capture 90% of the total estimated species richness are given in Table 2.9. Once again, the Linear Dependence model suggests most areas were adequately sampled, except for those where six samples or fewer were taken. An average of 13 samples are required to capture 90% of estimated species, with a range of 2 – 25 for the individual site and set-time combinations. The Clench model again provides much higher estimates for required sample sizes, ranging from 9 to 129 and averaging 60. The Clench model suggests that in the areas where most of our sampling took place – the main survey areas – we sampled between 70 and 90% of estimated total fish species.

Areas represented by a single gillnet set are not included in this analysis: they are night-time sets at Gitaza, Burundi (15 species, 10 of which were represented by a single specimen) and Kigoma, Tanzania - (7 species, 3 'singletons') and day-time sets at Kalambo (11 species, 6 singletons) and Chikonde, Zambia (2 species). We have also excluded from the set of graphs all site and set-time combinations with less than four replicate samples, as extrapolations from such small sample sizes are unreliable.

The results of the analysis of sampling adequacy presented in Table 2.9, Figure 2.11, Figure 2.12 and Figure 2.13 suggest that, with the gillnets used, a fairly large number of replicate sets should be set to ensure reasonable estimates of richness. Once again, the estimated required sample size is variable by area, and differs markedly according to which model is chosen to represent the best extrapolation of the likely consequence of additional sampling in terms of probability of sampling additional species. In most cases where sampling was adequate, the Clench model does appear to fit the species distributions better as the asymptote is approached (although the difference in fit is not statistically significant in any case, with r^2 values usually >0.99 for both models – see Appendix 8.3: Table 8.5). If the Clench model is accepted as being preferable, then future surveys should employ at least 60 gillnet sets per location, with required sample-sizes for areas like Nsumbu possibly being as high as 95 (Table 2.9). These estimates are of course specific to the gillnets used in this programme, and must be recalculated for each gear-type used – another incentive for moving towards standardisation of sampling methodology between surveys.

2.8.4 Sampling effort for molluscs

Sampling for molluscs was done by both SCUBA and dredge techniques. Dredging was not very successful, probably owing to the small mouth of the naturalist's dredge and the relative patchy distributions of sand-dwelling molluscs. Dredging was carried out only at Rusizi and Nsumbu. Dredge sampling effort data is not considered further here. Standardised mollusc searching events constitute the sampling unit for SCUBA surveys.

As the mollusc sampling was evolving as identification skills were developed and protocols refined, sample sizes were generally small. When making decisions on how to treat the dataset, i.e. whether to pool or subdivide data on the basis of substrate and/or depth we drew on field observations from BIOSSE surveys as well as previous sampling expeditions (K. West). Therefore, samples from each locality are subdivided by the five main substrate categories: sand, mixed (sand), mixed (rock), rock, and shell beds. In addition, depth categories were assigned based on broad subdivisions of the littoral zone (0m, 5-15m, >20 m), which seem to correspond to species depth zonation (West, 1997). As a result the number of replicates for each substrate depth-locality combination is rather low (Table 2.10).

Sample-species accumulation curves were plotted for each location-depth-substrate category combination for which three or more replicate transects were available (Figure 2.14 and Figure 2.15). The mollusc sampling protocols were developed after much trial-and-error, and had to await the development of a capacity to identify them within the BIOSSE team. This capacity developed as one of us (K. West) specialising in Lake Tanganyika molluscs was able to join the field teams in training and survey activities, and to produce field identification materials (West et al 2000). Molluscs thus tended to be under sampled, as illustrated in Figure 2.14. In the case of the sandy habitat at Uvira, no levelling off of the species accumulation curve was evident after 3 transects. Many depth-substrate-locality combinations had between 0 and 2 samples only, and are not analysed here.

Mahale NP was rather better sampled, and several depth-habitat-substrate categories provide sufficient replicate transects to fit models to species accumulation curves. Many of these curves do not, however, approach the estimated total species richness within the sampling effort applied (Figure 2.15). Only the mixed (Rock) sample at Mahale reaches a clear asymptote. This is indicative of a high degree of patchiness (and therefore uncertainty in whether or not additional species will be found in additional sample transects). For sandy substrates, it also reflects low density of the more conspicuous species.

Table 2.10 Number of replicate transects for mollusc species in each sampling strata (area, depth band, substrate category)

Country	Area	Substrate	Depth (m)	N
Burundi	Gitaza	Mixed rock	0	1
	Gitaza	Mixed rock	>20	2
	Gitaza	Mixed sand	>20	2
	Gitaza	Rocky	>20	1
	Gitaza	Sandy	>20	1
	Gitaza	Mixed sand	5 to 15	2
	Gitaza	Mixed rock	5 to 15	2
	Gitaza	Rocky	5 to 15	2
	Gitaza	Sandy	5 to 15	4
				17
DR Congo	Pemba, Luhanga, Bangwe	Rocky	0	2
	Pemba, Luhanga, Bangwe	Mixed rock	5 to 15	5
	Pemba, Luhanga, Bangwe	Rocky	5 to 15	4
	Pemba, Luhanga, Bangwe	Sandy	5 to 15	3
	Uvira	Mixed sand	0	2
	Uvira	Rocky	0	1
	Uvira	Rocky	5 to 15	1
	Uvira	Mixed sand	5 to 15	4
	Uvira	Sandy	5 to 15	3
				25
Tanzania	Mahale	Rocky	0	1
	Mahale	Mixed sand	>20	4
	Mahale	Sandy	>20	12
	Mahale	Shell	>20	5
	Mahale	Mixed rock	>20	2
	Mahale	Shell	5 to 15	1
	Mahale	Mixed rock	5 to 15	8
	Mahale	Rocky	5 to 15	9
	Mahale	Sandy	5 to 15	13
				55
Total samples:				97

Figure 2.14 Species accumulation curves (with standard errors) for mollusc diver-transect surveys in Burundi (Gitaza) and DR Congo (all other sites). Fitted asymptotic models (Linear Dependence and Clench) are also indicated.

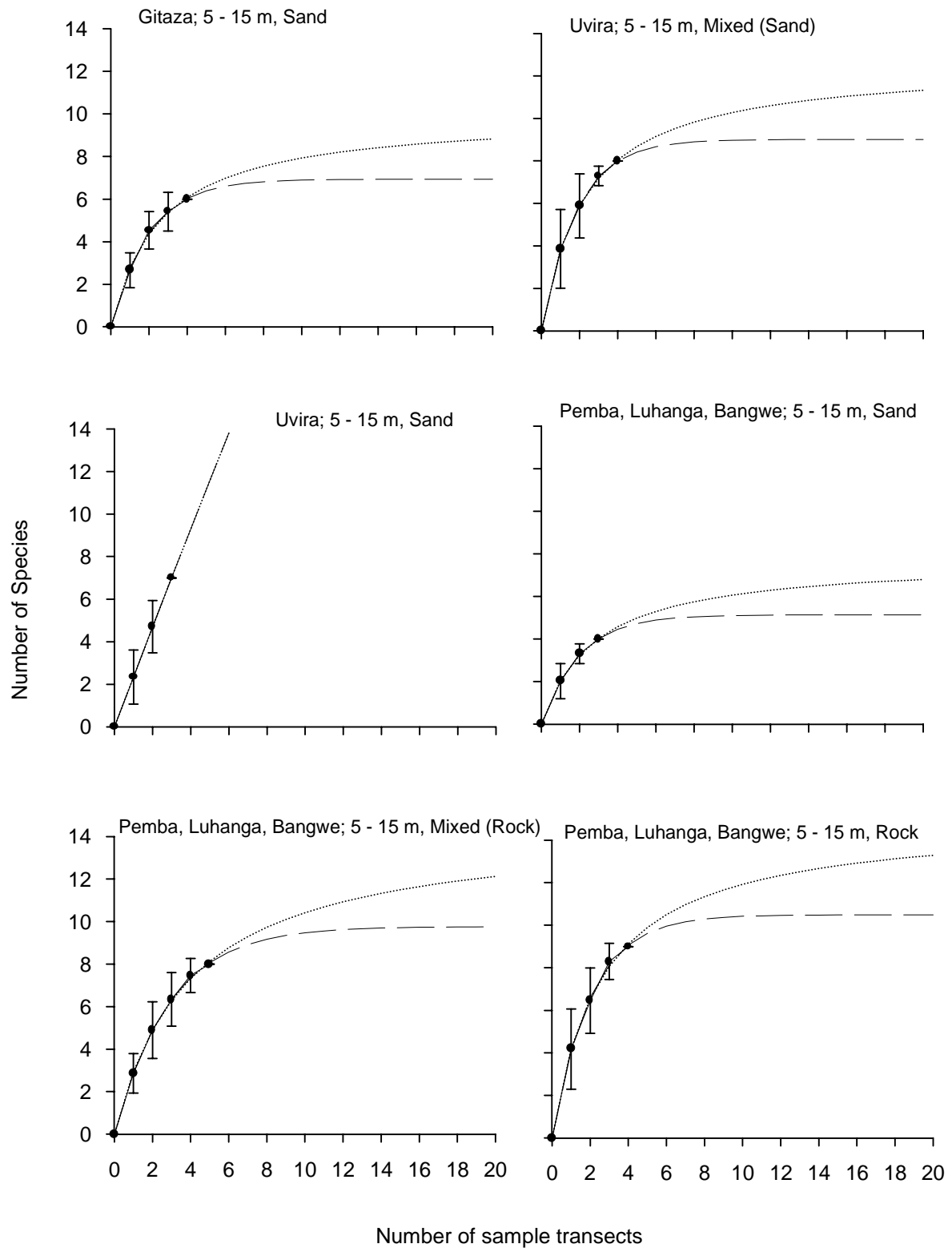
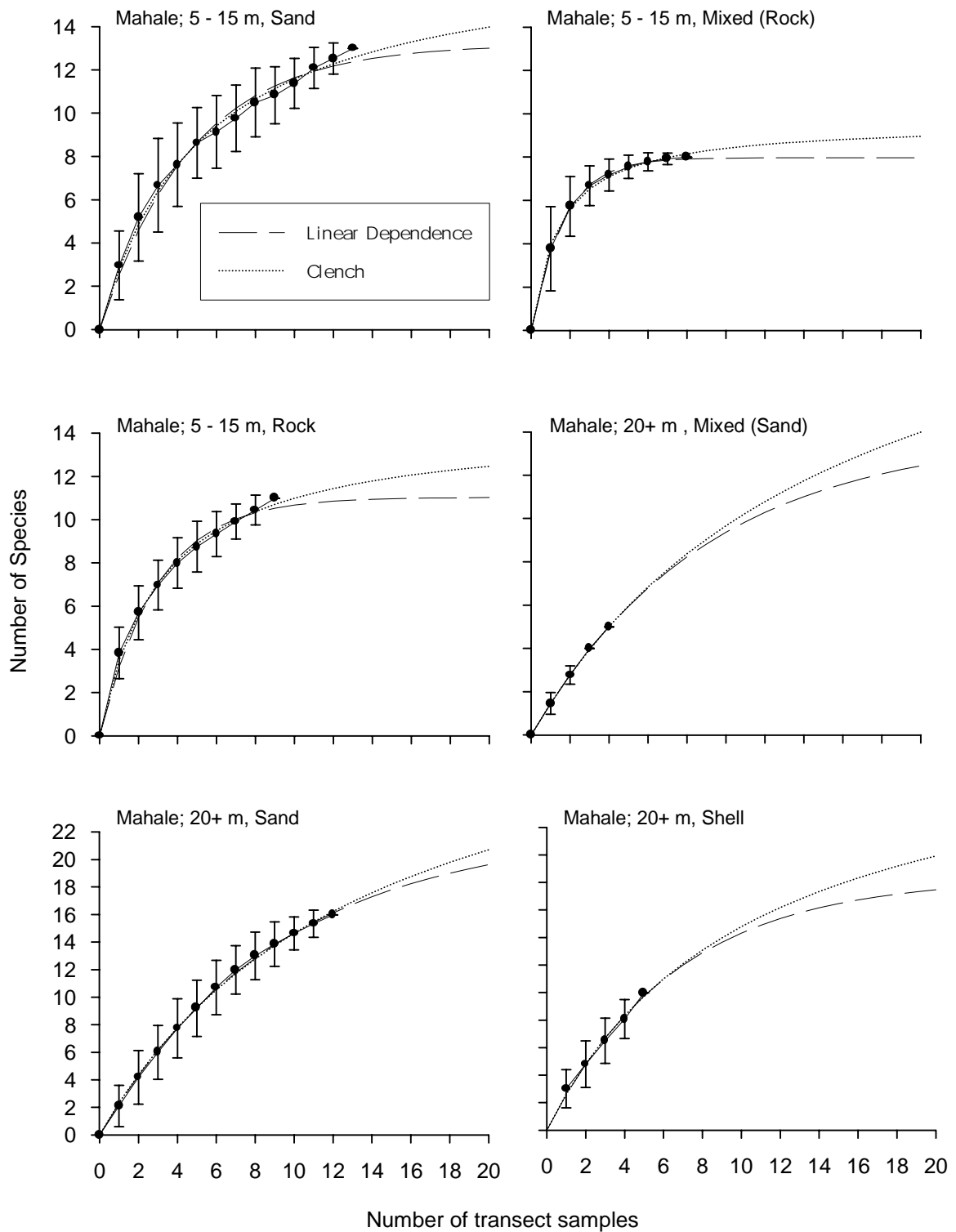


Figure 2.15 Species accumulation curves (with standard errors) for mollusc diver-transect surveys in the sub-littoral zone of Mahale National Park. Fitted asymptotic models (Linear Dependence and Clench) are also indicated. The Y-axis for the 20+ m sample from the sand and shell bed substrates has been plotted on a different scale for clarity.



Estimates of mollusc species richness are investigated in Chapter 4 (along with fish species richness estimates), however it is evident that relatively few species can be expected in surveys of the type undertaken, compared to fish surveys (Table 2.11). This means that relatively small differences in estimated species richness will have a large impact on calculated minimum sampling size required to census 90% of species present. Bearing this in mind, it is evident that for most sites, the present survey under sampled the extant mollusc diversity. According to the Clench model (which appears to fit the species accumulation curves better than the linear dependence model), some 20 to 35 transects for each sampling strata would be required to provide a strong probability of including 90% of the species present.

There is clearly a need for more intensive mollusc surveying, but there remain difficult sampling problems in dealing with the sand/rock matrix, and with species that vary in size by orders of magnitude, necessitating combined visual and mechanical sorting sampling techniques. There is also an element of learning involved in this type of survey work, where experienced workers can often find many more species than inexperienced ones, through development of a 'search image' and knowledge of micro distribution patterns and habitat preferences.

Table 2.11 Analysis of sampling adequacy for diver transect surveys of gastropod molluscs, using two asymptotic models (see text for details)

					Linear Dependence Model			Clench Model		
Area	Depth (m)	Substrate	N	S _{obs}	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})	S _{max}	S _{obs} :S _{max} (%)	N _{req} (90% S _{max})
BURUNDI										
Gitaza	5 to 15	Sand	4	6	7	86	5	10	60	23
DR CONGO										
Pemba etc	5 to 15	Sand	3	4	5	78	5	8	52	25
Pemba etc	5 to 15	Rock	4	9	10	86	5	15	60	23
Pemba etc	5 to 15	Mixed (Rock)	5	8	10	82	7	15	55	35
Uvira	5 to 15	Mixed (Sand)	4	8	9	89	4	13	63	20
TANZANIA										
Mahale	5 to 15	Sand	13	13	13	99	11	18	74	47
Mahale	5 to 15	Mixed (Rock)	8	8	8	100	4	10	83	13
Mahale	5 to 15	Rock	9	11	11	100	7	14	76	28
Mahale	> 20 m	Sand (Mixed)	4	5	14	36	21	25	20	145
Mahale	> 20 m	Sand	12	16	22	72	21	35	45	127
Mahale	> 20 m	Shell	5	10	18	55	15	30	33	96

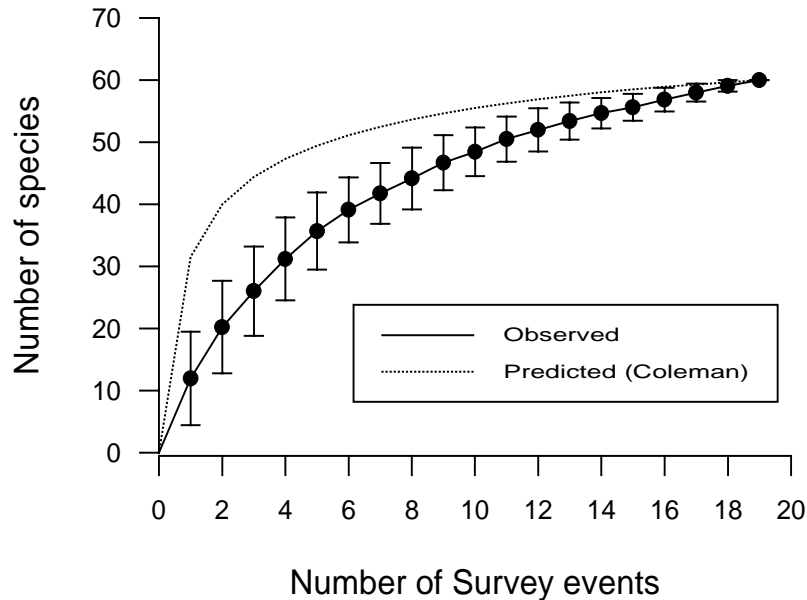
N = number of SVC samples, S_{obs} = observed number of species in those samples, S_{max} = estimated species richness, N_{req} = the number of samples that would be required to sample 90% of the estimated species present. Note that estimates of S_{max} and $S_{obs}:S_{max}$ are rounded to the nearest integer but that the calculations of have been made with the original un-rounded estimates.

N.B. – the sample from Uvira, 5-15 m, Sand, is excluded from the analysis as both models failed to reach an asymptote at realistic species numbers

2.9 Assessing sample heterogeneity

One of the key factors in determining potential bias in the estimates of species richness from incomplete or under sampled datasets is in assessing whether the sample groupings are reasonably homogenous.

a) *Stationary visual fish census, sandy substrates, Mahale National Park*



b) *Stationary visual fish census, rocky substrates, Mahale National Park*

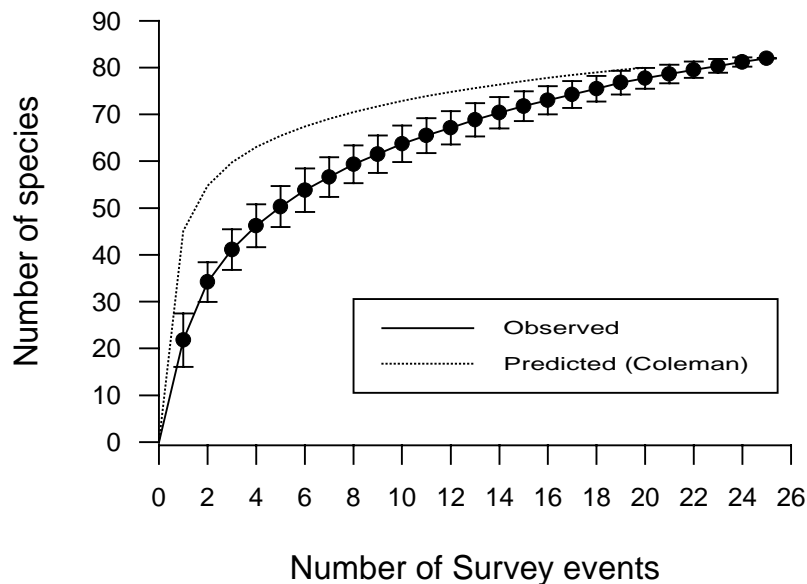


Figure 2.16 Comparison of observed species-sample accumulation curves (based on 100 randomisations of the data, with standard deviations) and calculated Coleman or 'random placement' curves.

One way to examine the level of homogeneity is to compare the empirical mean randomised species accumulation curve with the curve expected if the individuals in all samples pooled had been randomly assigned to the samples. If this expected curve rises significantly more

steeply from the origin than the mean empirical curve, then the empirical samples are more heterogeneous in species composition than sampling error, alone, can account for (Colwell and Coddington, 1994).

Figure 2.16 illustrates that there is more heterogeneity in the datasets than can be accounted for by random error variation alone. There is an important trade-off to be made in all analyses, between differentiating samples within known environmental gradients (depth, substrate type or habitat) and between accumulating sufficient samples to provide a reasonable analysis of total richness within a locality. Ideally, we would have large sample-sizes within each depth-substrate combination. In practice, we have had to pool samples across broad habitat categories and depth ranges to make any evaluation of minimum required sampling sizes and estimated total species richness. We have to accept a reduction in precision in estimates of species richness, and a reduction in our ability to elucidate links between specific habitat types and fish and mollusc communities. For fish, we have pooled to a greater extent than for molluscs, because habitat-species assemblage relationships are more likely to be very strongly coupled in benthic invertebrates than in the more mobile fish species.

As samples accumulate, through future surveys, it should be possible to reduce the amount of pooling, and obtain more reliable estimates of true species richness by extrapolating from data sets of greater homogeneity. Certainly it is desirable **not** to pool across known environmental gradients whenever possible. However, given that the primary objective here is not to carry out ecological studies of species-habitat association, but to provide preliminary estimates of species richness of large areas for conservation planning purposes, pooling to increase sample sizes for each area is justifiable.

2.10 Testing for complementarity and bias in different sampling techniques

2.10.1 Fish Sampling methods

Every fish survey method will be subject to bias (Perrow *et al.*, 1996). If the results of sample surveys are to be used comparatively, then the extent and nature of bias must be investigated. This can be done by simple comparative analysis of the species compositions of different survey techniques used in the same area.

Two types of qualitative comparison are employed here as a preliminary analysis. First, we computed lists of species caught uniquely by each survey method employed (gillnet-day, gillnet-night, SVC, RVC) and calculated simple similarity indices:

$$\text{Similarity} = \frac{2c}{a + b} \quad \text{Krebs, 1978.}$$

Where a = number of species in sample A, b = number of species in sample B and c = number of species common to both A and B.

A high similarity index indicated that the use of either survey method would include most species present, a low similarity index would indicate that it was necessary to use both methods to survey the fish population adequately. This gives an indication of the types of fish that could be missed in surveys that do not employ the full range of techniques, but is sensitive to the appearance of rare or infrequent species, and assumes comparable sampling effort.

Second, we created a list of the 10 most abundant species recorded by each quantitative survey method (gillnet-day, gillnet-night, SVC). By comparing which species are most abundant in each survey method, we could gauge whether different techniques were sampling different sections of the same fish community.

2.10.2 Comparing gillnet catches by day and night, Rusizi

Night time-gillnets tended to catch more species than daytime set gillnets (Figure 2.11, Figure 2.12 and Figure 2.13: Table 2.9). In Rusizi, for example, 59 species were recorded from 23 hauls in the daytime, while 18 hauls sampled 72 species at night. Although it must be noted that daytime soak times for the gillnets were lower than during the night (a total of 138 hours in the day, 270 at night), we have established that there does not appear to be a relationship between soak time and catch rates in terms of either species or number of individuals caught, within the range of soak times used in this survey programme (Figure 2.10).

The number of species caught uniquely by day or night is low compared with the total diversity, so there is a relatively high Krebs similarity index (0.83, see Table 2.12). Of the 14 species caught uniquely at night several are nocturnally active catfish or deepwater cichlids that move into the shallows to feed at night (*Auchenoglanis*, *Bathybates*, *Hemibates*, *Benthochromis*, *Synodontis*, *Chrysichthys*, etc ...). The list of species caught only during the day is shorter (only 4 species). Their presence only during the day is likely to be by chance, with the possible exception of *Perissodus microlepis*, which feeds by attaching other fish, tearing off a piece of flesh or scales, and may favour daylight to help it hunt.

Table 2.12 Species caught uniquely in day and night set gillnets, Rusizi, Burundi, synthesised from all sets

DAY Number of sets=23 Total species recorded =59		NIGHT Number of sets = 18 Total species recorded =72	
1	<i>Chrysichthys brachynema</i>	1	<i>Astatoreochromis straeleni</i>
2	<i>Lestradae perspicax</i>	2	<i>Auchenoglanis occidentalis</i>
3	<i>Perissodus microlepis</i>	3	<i>Bathybates graueri</i>
4	<i>Xenotilapia burtoni</i>	4	<i>Benthochromis tricoti</i>
		5	<i>Chrysichthys platycephalus</i>
		6	<i>Cyathopharynx furcifer</i>
		7	<i>Enantiopus melanogenys</i>
	Similarity index = 0.83	8	<i>Hemibates stenosoma</i>
		9	<i>Neolamprologus mondabu</i>
		10	<i>Neolamprologus tetracanthus</i>
		11	<i>Petrochromis fasciolatus</i>
		12	<i>Plecodus paradoxus</i>
		13	<i>Synodontis multipunctatus</i>
		14	<i>Trematocara nigrifrons</i>
One sampling unit = 60 m multimesh gillnet set overnight (15 hours) or during the day (6 hours).			

While there may be over 80% overlap between day and night catches, the most striking difference between day and night samples is in the structure of catches (Figure 2.17). The most abundant species in the daytime catches (*Boulangerochromis microlepis*) does not feature among the dominant species in night-time catches. *Lates* species are similarly common in night-time catches but not in daytime ones. However five species feature in the 'top ten' most abundant species in both day and night catches (Figure 2.17). From this we can conclude that night-time gillnetting is slightly more effective and is likely to add nocturnal and crepuscular species, while retaining most species caught during the day. We therefore recommend that gillnetting for species richness estimation be carried out by night where possible.

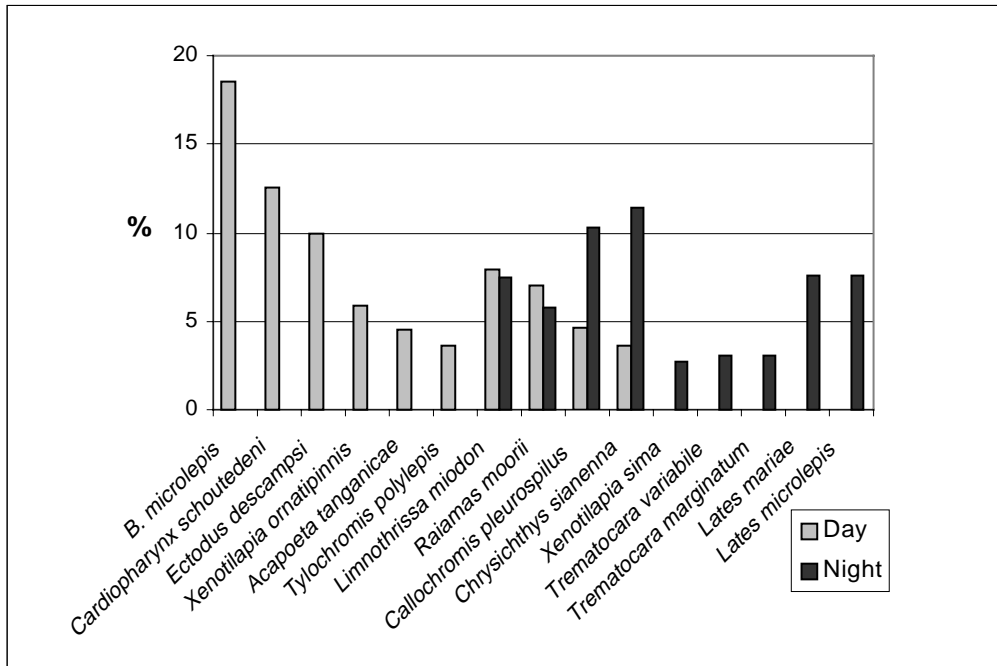


Figure 2.17 The ten most abundant species represented in day and overnight gillnet samples from Rusizi

2.10.3 Comparison of gillnet, SVC and RVC samples from Mahale National Park

As it was not possible to sample all sites with the same methods, and as ultimate species lists are compiled from combinations of sampling methods, it is of interest to establish biases and complementarities between different sampling methods. We use the survey of Mahale National Park to explore the selectivity of different methods, as Mahale was comprehensively surveyed over a short time period using all three main fish sampling techniques – SVC, RVC and gillnetting.

It is evident that gillnets sample fish normally found in deep water but feeding at night in the shallows (*Bathybates sp*, *Chrysiichthys sp*, *Trematocara sp*, *Tanganykallabes*). These are not seen in daytime dive-surveys in shallow water (Table 2.13). The lists of species seen uniquely by SVC and RVC methods are not obviously differentiated from one another (and indeed similarity indices between these two methods are high). Thus it would appear that the most efficient sampling strategy would be to combine gillnetting with either SVC or RVC, and that there is little advantage to be gained by using both SVC and RVC in the case of Mahale, as both recorded almost the same number of species (103 and 104).

Four of the ten most abundant species in gillnet catches also occur among the most abundant diver counts in the SVC method (Figure 2.18). The differences probably reflect differences in behaviour, with more mobile and predatory species being preferentially selected by gillnets, while static and cryptic species tend to be better sampled by careful visual census, such as in the SVC technique. The two techniques are therefore complementary, and the closest approximation to actual species richness can be achieved by using both techniques with sufficient replicates to ensure most species vulnerable to sampling by each method is included in any census.

It should be noted that the continuing slow accumulation of species seen in the species-abundance curves may represent species that are not efficiently sampled by one or other method, rather than being rare. Thus, an area that is apparently under sampled by both gillnets and SVC may be adequately sampled by the combination of the two methods.

Table 2.13 Species recorded uniquely in rapid visual census (RVC), stationary visual census (SVC) and night-set gillnets (GILL), Mahale, March-April 1999.

	RVC Number of transects = 108 Total species recorded = 104		SVC Number of surveys = 78 Total species recorded = 103		GILL Number of sets = 29 Total species recorded = 96
1	<i>Aethiomastacembelus cunningtoni</i>	1	<i>Altolamprologus calvus</i>	1	<i>Batybates graueri</i>
2	<i>Aethiomastacembelus platysoma</i>	2	<i>Caecomastacembelus ophidium</i>	2	<i>Batybates horni</i>
3	<i>Barbus sp</i>	3	<i>Neolamprologus falcicula</i>	3	<i>Batybates leo</i>
4	<i>Cæcomastambelus frenatus</i>	4	<i>Neolamprologus niger</i>	4	<i>Batybates vittatus</i>
5	<i>Julidochromis ornatus</i>	5	<i>Oreochromis tanganicæ</i>	5	<i>Benthochromis tricoti</i>
6	<i>Julidochromis tanscriptus</i>	6	<i>Telmatochromis caninus</i>	6	<i>Callochromis macrops</i>
7	<i>Neolamprologus olivaceous</i>	7	<i>Xenochromis hecqui</i>	7	<i>Chrysichthys brachynema</i>
8	<i>Petrochromis ephippium</i>			8	<i>Chrysichthys platycephalus</i>
9	<i>Spathodus erythron</i>			9	<i>Chrysichthys sianenna</i>
10	<i>Telmatochromis burgeoni</i>			10	<i>Cyprichromis nigripinis</i>
11	<i>Xenotilapia papilio</i>			11	<i>Hyppopotamyrus discorhynchus</i>
			Similarity indices: RVC/SVC = 0.85 SVC/GILL = 0.71 GILL/RVC = 0.68	12	<i>Limnothrissa miodon</i>
				13	<i>Petrochromis sp(red)</i>
				14	<i>Phyllonemus filinemus</i>
				15	<i>Synodontis eurystomus</i>
				16	<i>Tanganicallabes mortiauxi</i>
				17	<i>Trematocara caparti</i>
				18	<i>Trematocara marginatum</i>

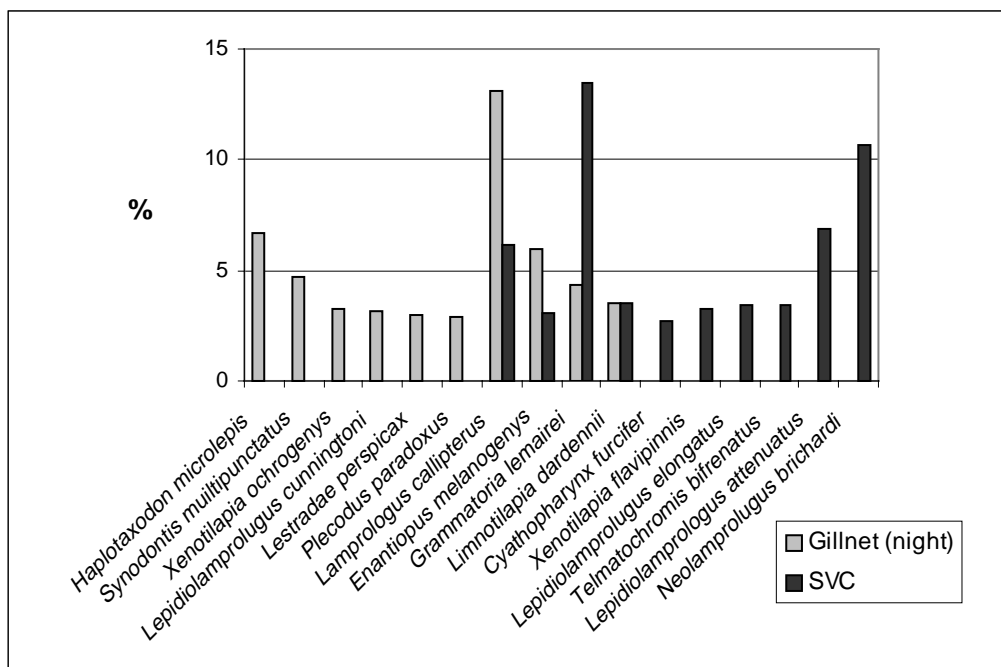


Figure 2.18 The ten most abundant species in gillnet and SVC surveys, Mahale Mountains National Park

2.10.4 Mollusc sampling methods

Because we experimented with dredging relatively late in our program, there was insufficient data to compare species richness as a function of survey method (dredging or diving). However, surveys completed in Zambia allow comparison between the sampling efficiency of divers and dredging. These comparisons are limited to soft substrate surveys, as dredging was not attempted (and is generally not feasible) on hard substrates where the equipment can get caught or torn. A comparison of which soft-substrate-dwelling molluscs were found in Zambia by each method provides a first insight into the relative selectivities of each method.

Table 2.14 Soft-substrate-dwelling mollusc species lists found in Zambia by diving and by dredging

Diving	Dredging
	<i>Bathanalia howesi</i>
	<i>Caelatura spp</i>
	<i>Limnotrochus thomsoni</i>
<i>Neothauma tanganyicense</i>	<i>Neothauma tanganyicense</i>
<i>Paramelania minor</i>	
	<i>Syrnolopsis lacustris</i>
	<i>Syrnolopsis minuta</i>
	<i>Tanganyicia neritinoides</i>
<i>Tanganyicia rufofilosa</i>	<i>Tanganyicia rufofilosa</i>

Interestingly, dredging recovered three very small species (*Tanganyicia neritinoides* and the two *Syrnolopsis* species) while divers did not recover any small species. Dredging may be a more efficient way of surveying small molluscs as the dredge 'samples' a much larger area than divers do when they sieve sediment.

Dredging recovered more species from soft substrates than divers. Unfortunately, because we did not dredge and dive at the same locality, we cannot know for sure if this is a function of disjunct distribution patterns. Future studies should dredge and dive at the same locale to eliminate this variable and test whether the two methods do recover similar taxa.

2.11 Evaluation of biodiversity assessment methods

In this chapter, we have highlighted the questions we set out to answer and the strategy we adopted to collect the data necessary to answer them. We have given an overview of the philosophy that guided our approach, and an overview of the process of developing a methodology for biodiversity assessment that takes into account survey objectives, institutional and human resource capacity and the practical realities of fieldwork on Lake Tanganyika.

We have also tested and compared our methods to enable us to account for biases in different techniques, and to assess, and provide guidance on, the minimum sample sizes required for valid comparative studies. This preliminary analysis and testing was also necessary to define sub-sets of data on which to base subsequent analyses.

We conclude that not all our sampling has been adequate to provide reliable estimates of species richness for all sites sampled. We would argue, however, that we have achieved good coverage of our main sampling areas, including the four proposed and existing National Parks, and at least three areas considered adversely impacted by pollution and sedimentation (Uvira, Bujumbura Bay, Mpulungu). The strength of this study is that it has attempted to investigate the sampling requirements for biodiversity assessment. It has shown that such requirements are highly variable, depending on the structure of communities, patchiness of the habitat and on the species richness itself.

The type of species-accumulation curve represented by the Clench model is most typical of large areas of high biodiversity. It assumes that the probability of adding species to the list decreases with the number of species already recorded, but increases over time (or sampling

effort). Soberón and Lorente (1993) recommend this model for larger areas than those where the linear dependence model would be applied, or for taxa for which the probability of adding new species will increase as more time is spent in the field. The Linear Dependence model is perhaps better suited to sampling a known diversity of species in a relatively small study area or habitat. This does suggest that to gain reliable estimates of total species richness will require very extensive sampling programmes at each location to be compared. Data from casual collecting visits such as those undertaken by earlier studies are therefore unlikely to represent useful estimates of species richness.

These analyses are preliminary, and much further refinement is possible, particularly in the calculation of different similarity indices between fish communities found at different combinations of depth, substrate type, sampling method and location of sampling. We hope that the availability of the data in the region will stimulate scientists in the participating institutions to undertake further, more refined analyses. In particular, we recommend the calculation of quantitative measures of similarity, such as the Merista-Horn index, now greatly facilitated by the availability of appropriate software for this type of analysis (e.g. Pisces Conservation Ltd, Species Diversity and Richness II, 2000). This will allow objective decisions to be made on whether it is best to pool samples across known environmental gradients in order to increase sample size, or to accept under sampling and use model extrapolations of species richness for comparative purposes.

Although we have made considerable progress towards identifying biases and uncertainties in sample surveys, there is more work to do in this area, and future surveys will need to take into account the findings of our work on minimum required sample size and effort. The present survey results are confounded to some extent (but it is a quantifiable extent) by the limitations of differing and sometimes inadequate sampling size. It has also been impossible to eliminate sampling biases, for example in the use of non-comparable sampling methods between areas where diving was or was not possible. All survey activities that aim to sample across habitat types and species groups will be confounded by these difficulties (which is why comparative all taxa biodiversity inventories are almost impossible to achieve). We hope that the experiences detailed here will aid the design of future surveys, where adequate sample size and comparable methodology can be allied to carefully focused and defined survey aims to improve the quality of information available for management decision-making.

A particularly useful feature of this analysis, not previously undertaken in Lake Tanganyika, is our use of species accumulation curves to give measures of the completeness of our biodiversity surveys. This allows a comparison of species richness between localities, and provides an assessment of trade-off of increased sampling cost and effort versus returns in the form of additional information (Henderson and Southwood, 2000).

2.12 Alternative methods of biodiversity assessment

The methods of assessment chosen by this study are the conventional species-based approaches used in many such surveys. This is despite well-known concerns with the definitions of species, and species concepts themselves (e.g. Mishler and Donoghue, 1982; Turner, 1999; Wheeler and Meier, 2000), a growing consensus that species diversity is not the most important diversity-related attribute of an ecosystem (Bengtsson, 1998; Schwartz et al 2000) and a move away from species-based conservation practice to broader focus on environmental conservation (Pickett et al., 1997).

The choice of conventional species-based measures of diversity has both advantages and disadvantages. The main advantages are that the results will be comparable with past and future surveys of the same type, and the survey outputs are likely to be broadly acceptable to administrators impressed by long lists of Latin names, and scientists reassured by the legitimacy these names confer.

The disadvantage of using conventional taxonomic-based measures of biodiversity is that the limited knowledge of formal taxonomy of Lake Tanganyika organisms, and the scarcity of specialists in possession of that knowledge, was always going to constrain the number of taxonomic groups that could be chosen for survey. The most extensive previous surveys

have sampled three groups: fishes, molluscs and ostracods (Cohen *et al.*, 1993; Alin *et al.*, 1999), whereas we have only sampled fishes and molluscs. At present, there is insufficient taxonomic expertise among riparian nationals to include ostracods in routine surveys. In short, there were few options for acceptable 'total biodiversity surrogates', and an 'all taxa biodiversity inventory', although of potential scientific interest, would not have been feasible nor useful in management terms (Kaiser, 1997).

Increasing the level of taxonomic knowledge in Lake Tanganyika was one potential BLOSS objective (it was never an LTBP objective), but was difficult to achieve on a time-scale relevant to meeting the project's needs to develop advice for management within its 5 year lifespan. BLOSS achieved something in this field: there is now a cadre of 23 research scientists and technicians in the institutions of all the riparian countries with the ability to identify a high proportion of the lake's fish and mollusc species. This is an improvement on the situation before the project, when perhaps 10 scientists on the lake (mostly in Burundi and Congo, with some knowledge in Zambia) could identify fish, and none could identify molluscs. There are also 20 qualified scientific divers, who have amassed considerable experience of quantitative underwater survey techniques. These skills could be built on when extending surveys to new taxonomic groups in future.

Even this expanded scientific capability is limited when faced with the size of the lake and the diversity of its biota. The limitations of conventional, formal species-based survey approaches was appreciated early on in the project and other, more radical, methods of assessing relative biodiversity and conservation value were proposed at the time. These suggestions included approaches commonly used in major biodiversity projects elsewhere:

1. *The use of non-specialist technicians as 'parataxonomists' to distinguish morphologically 'recognisable taxonomic units' (Oliver and Beattie, 1993; 1996a; 1996b) for sorting large samples.* Expert time is expensive and there is not enough time and experts available to carry out the large amount of routine sample processing required of comparative biodiversity surveys. Trials with insect species showed that with a few hours training, non-specialist technicians and students performed with 87% accuracy compared to formally trained taxon-specialists (Oliver and Beattie, 1993). This level of accuracy may be inadequate for the production of a definitive monograph, but is likely to suffice for purposes of conservation management, where error variances and bias associated with sampling techniques are likely to over or under-estimate species richness by greater margins. Most major biodiversity projects in rainforests, where the task of species identification is at least as complex as Lake Tanganyika, make extensive use of veritable armies of parataxonomists (Tangley, 1990; Cranston and Hillman, 1992; Kaiser, 1997).

2. *Participatory biodiversity assessment and monitoring.* Fishermen generally have a great deal of non-scientific or 'indigenous knowledge' about fish species. Given the diversity of fishing methods in use in all habitats of the lake (Lindley, 2000) there is a strong probability that there are some fishermen in the lake who, between them, could identify the majority of fish species. A distinguished African Great Lakes scientist recently highlighted that many of his early scientific descriptions and ecological insights into cichlid fish in Lake Malawi were based on observations grounded in local knowledge (Fryer, 1999). Colonial-era scientists seemed to make greater use of local knowledge than subsequent fishery experts have done. Worthington, who visited Lake Victoria in 1927 to carry out biological research in support of fisheries development, narrates:

"In addition to the fish themselves, I became deeply interested in the indigenous native fishing methods and was surprised at their variety....adapted to what was a clear understanding of the fish themselves."

"The Luo fishermen we employed had a better eye for a species than we had and pointed out that the "ngege", as served for breakfast in Nairobi, was in fact new to science"

pp 659-660 in Worthington (1996)

Involving fishermen and other lakeshore people in biodiversity assessment and monitoring has other advantages besides being a cost-effective use of existing information. It minimises the requirements for expensive expert input; it involves resource-users, who have a larger stake in the future of the resources than any government official or visiting scientist; and it serves to maintain dialogue and build co-operative understanding between resource users, researchers and resource managers. The importance of using indigenous understanding of natural resource systems to assess, manage and monitor natural resources, including biodiversity (e.g. Hellier *et al.*, 1999), is now widely recognised (see a review by Sillitoe, 1998) beyond the boundaries of ethnobotany where it has long been a legitimate research method (Martin, 1995). The perils of ignoring indigenous ecological understanding, and the price of 'expert arrogance' are legitimate targets for criticism in much recent writing on environmental conservation in developing countries (Brokenshaw *et al.*, 1980; Agrawal, 1995).

3. *The use of higher-taxon approaches.* If the hierarchical taxonomic classification system has any objective validity, then it is obvious that higher levels of taxa provide integrative summaries of diversity within each level of classification. Thus, in principle, any level of taxonomic classification can be chosen for comparative analysis. By convention, the species level is chosen, but where identification to species is not possible, it is common to use higher-taxon approaches. There is some experience indicating that correlation between diversity at different taxonomic levels can be established (Balmford *et al.* 1996), although this is likely to be highly variable (Gaston and Williams, 1993; Williams and Gaston, 1994; Prance, 1994; Anderson, 1995). Balmford *et al.* (1996) found that using woody plant genera and families, rather than species, yielded comparable estimates of relative conservation value of tropical forest, for 60-85% less cost than a species-based survey. Exploration of area-specific relationships between generic or family-level diversity and species diversity would be worthwhile. It may be possible to use a much wider range of taxa, for lower sample processing effort, if the principle of higher-taxon comparisons proves acceptable. Biotic indicators of ecosystem health (which should be related to diversity) in aquatic systems are usually based on identification of macroinvertebrates to higher taxonomic levels, such as genus or family (Chessman, 1995; Hilsenhoff, 1988).

4. *Rapid assessment techniques.* In recognition that the task of determining a conservation strategy is urgent in areas where biodiversity is both threatened and poorly known or difficult to survey, a number of techniques for rapid assessment of conservation value have been developed (reviewed in Groombridge and Jenkins, 1996). These techniques, which employ some of the approaches outlined above, vary in their data requirements, cost, and suitability for application for different purposes and at different spatial scales. The methodology developed here is most closely related to the 'Rapid Assessment Programme', developed by Conservation International for surveys of poorly known areas using 'surrogate' or 'indicator' groups identified to species level by small teams of national and international experts (See Table 3.2 in Groombridge and Jenkins, 1996.). These surveys are then used to assess conservation value by assuming a relationship between these 'indicator' groups and total diversity and habitat quality. The main drawbacks of the methodology are the reliance on specialist taxonomic expertise (beyond standard field identification skills) and the assumptions made about relationships between indicator diversity and total diversity.

Other rapid assessment methods include Conservation Biodiversity Workshops, Conservation Needs Assessments, Gap Analysis and Biodiversity Information Systems (Groombridge and Jenkins, 1996). Some of these methods do not require additional survey work, and aim to make best use of existing information, including socio-economic data that can be overlooked by biodiversity specialists. The BLOSS studies included elements of these procedures, particularly in its work towards setting up Biodiversity information systems. The Transboundary Diagnostic Analysis and Strategic Action Programme processes contributed elements of the Conservation Needs Assessments approach, and Cohen's (1991) International Conference on the Conservation and Biodiversity of Lake Tanganyika provided an exemplary illustration of the Conservation Biodiversity Workshop approach.

When aired at the start of the present project, many of the above suggestions for formalised 'rapid' techniques of assessment met with considerable scepticism from scientists familiar with Lake Tanganyika. We maintain that the realities of practical conservation work and the

need to deliver relevant and timely advice to policy makers remain compelling reasons for open-minded consideration of these techniques for future surveys.

We stress that the choice of assessment strategy has been a learning process for all of us involved in this study, and that we are satisfied that we have made good decisions over methodology, and that we have validated our chosen methods to produce useful data. We also recognise, however, that the quantity and range of data has been limited by the need to satisfy scientific criteria (international taxonomic standardisation, comparison with work done by scientists from outside the region) that are not closely related to the immediate project objectives. We offer these insights into less conventional approaches to biodiversity assessment to encourage those involved in future surveys to consider all options seriously. Such consideration should be based on adequate research of available alternatives and explicit consideration of relevant management goals. Groombridge and Jenkins (1996) provide an accessible introduction to the range of techniques that have been applied by others working in remote tropical locations of exceptional biodiversity interest, with limited resources and poorly known flora and fauna.

Our remaining concern is that, while we have a valid scientific methodology for biodiversity survey that meets the needs of the present project and is within the current capabilities of the riparian institutions, there is no backup method should the current capability change, due to staff changes, equipment failure or lack of funds. SCUBA diving demands specialist equipment, expertise and levels of funding that are high relative to local institutions' research budgets. Some of the methods proposed above are more robust and sustainable.

2.13 Summary

Chapter 2 has detailed the rationale, process and methodology developed for assessing biodiversity in Lake Tanganyika for the purposes of conservation and management planning. These analyses are intended to demonstrate that great care must be taken in designing and analysing simple species richness data. Assessing and quantifying bias is an important and neglected step in the analysis. In this case, it has pointed to a number of shortcomings with the present data set. These are principally that the 'completeness' of surveys is highly variable, and that it has been necessary to compare richness between areas sampled by pooling different techniques. It is not possible to correct completely for these problems. Although estimates of how many species remain unsampled can be (and have been) made, it is obviously not possible to identify which species they are. This remains a problem when undertaking complementarity analysis (Chapter 5). At this stage it is only possible to add a note of caution to such comparisons, and to urge those undertaking future surveys for comparative biodiversity analysis to take such considerations seriously. Despite these remaining problems, we believe that the present analysis complements and adds significantly to the more qualitative surveys previously undertaken. A summary of these previous surveys is reported in the next chapter.

For future surveys that aim to characterise species richness in areas to be compared for conservation prioritisation we recommend the following minimum sampling sizes and combination of survey techniques:

- RVC – 40 replicates per survey stratum (e.g. area between 5 and 15 m depth)
- Gillnet – 60 night-time sets with 60m multimesh nets per survey area
- Mollusc transects – 30 per survey stratum (chosen depth-habitat combination)

The SVC technique takes a similar amount of time to RVC, but covers less ground and samples a similar number or fewer species, with few that are unique (not found in RVC or gillnets). Its advantage is that it allows abundance to be estimated, so diversity indices can be calculated. However diversity indices are not necessarily more useful than species richness estimates for conservation prioritisation exercises, and are often calculated merely because it is traditional and relatively straightforward to do so, rather than for any directed purpose (see Chapter 4).