ECOLOGICAL ASPECTS OF THE MACROINVERTEBRATES ASSOCIATED WITH TWO SUBMERSED MACROPHYTES IN LAKE KARIBA

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DECLARATION

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ABSTRACT

Lagarosiphon ilicifolius Obermeyer and *Vallisneria aethiopica* Fenzl are the most common and abundant submerged macrophytes in shallow inshore waters of Sanyati Basin, Lake Kariba. *Lagarosiphon* is structurally more complex than *Vallisneria*. This study considered the macroinvertebrate assemblages associated with the two plant species with respect to (i) differences in structural complexity, (ii) predator-prey interactions and (iii) water physicochemical conditions.

A total of fifty-six macroinvertebrate taxa were obtained in an assessment of macroinvertebrates associated with *Lagarosiphon* and *Vallisneria* in shallow inshore waters ($\leq$ 1m) of Lake Kariba. Generally, there were no significant differences in macroinvertebrate assemblage composition, richness and diversity between the two macrophytes. However, the abundances of most taxa and overall macroinvertebrate abundance were significantly greater on *Lagarosiphon* than on *Vallisneria*. The assessment of body-size class distributions showed that a significantly greater proportion of large individuals of the mayfly *Cloeon* sp. occurred on *Lagarosiphon* compared to *Vallisneria*, while a greater proportion of large individuals of predatory coenagrionid naiads occurred on *Vallisneria* than on *Lagarosiphon*. The occurrence of greater proportion of large-sized individuals of *Cloeon* on *Lagarosiphon* was probably because the greater morphological complexity of *Lagarosiphon* reduced foraging success of invertebrate and fish predators on *Cloeon*. Conversely the simpler morphology of *Vallisneria* led to greater predatory effects such that predation on small-sized coenagrionid naiads by larger sizes resulted in a smaller proportion of small-sized naiads on *Vallisneria* compared to *Lagarosiphon*.

The effect of habitat variation on epiphytic macroinvertebrate assemblage was also assessed with respect to variation in the density cover of *Lagarosiphon*. The macroinvertebrate assemblage composition was not significant different among low-, moderate- and high-density beds. This suggests that the impact of fish predation was uniform across the vegetation density spectrum. The largest size class of *Cloeon* were present only in high density beds, while for Coenagrionidae, the largest individuals were obtained from low- and moderate-density beds and were absent in high-density beds. The study showed that variation in the density of *Lagarosiphon* has minimal effect on macroinvertebrate taxa composition but affects the body size distribution of some taxa through its effect on predator-prey interactions.

The effect of differences in morphological complexity between *Lagarosiphon* and *Vallisneria* on macroinvertebrate assemblages was also assessed experimentally in ponds. In the absence of fish predation when the plants grew in separate ponds, the number of insect taxa, diversity and abundances were significantly greater on *Lagaroshon* than on *Vallisneria*. In ponds in which the plants grew along side each other the total insect abundance on *Lagarosiphon* was significantly greater than on *Vallisneria*. The insect assemblage on both plants was dominated by anisopteran naiads. *Hemicordulia*, *Diplacodes* and *Trithemis* were the most dominant taxa on *Lagarosiphon* in single plant ponds. *Hemicordulia* and *Diplacodes* were absent from ponds comprised exclusively of *Vallisneria*, but *Trithemis* dominated and made up nearly 70% of the insect assemblage. In ponds that were cultured with both plants,

four anisopteran taxa, *Hemicordulia*, *Diplacodes*, *Trithemis* and *Tramea* were collected from both plants. Assessment of body-size class distribution showed that in single plant ponds, the anisopteran naiads on *Vallisneria* were characterised by a narrow range of size classes. Contrary, the body-size class distribution associated with *Lagarosiphon* had a much broader range of size classes. The study showed that the greater structural complexity of *Lagarosiphon* compared to *Vallisneria* allowed for the coexistence of a greater number of odonate taxa and broader range of their size classes, probably by reducing the intensity of intra-guild predatory interactions.

In another pond experiment large mobile predatory invertebrates were dominant in the absence of fish and reduced the abundances of small invertebrate taxa on both *Lagarosiphon* and *Vallisneria*. Adding predatory fish had a profound effect on macroinvertebrates on both plants. After fish were added, size-selective predation by fish resulted in the dominance of small-bodied invertebrate taxa on both plants. Total macroinvertebrate abundance on *Vallisneria* was significantly reduced after fish were added, but adding fish had no significant effect on overall macroinvertebrate abundance on *Lagarosiphon*. A study on the effect of small sizes (< 5 cm) of juvenile *Oreochromis niloticus* on different size classes of the damselfly *Ischnura* sp. showed that large-bodied naiads (>10 mm) were more vulnerable to fish predation and their percent survival was much lower than small- (< 5mm) and moderate-sized naiads (5–10 mm) even at low fish densities. Small-sized naiads were generally more susceptible to fish predation than moderate-sized ones probably due to intraspecific interactions such as cannibalism, which made them more active and so prone to fish attack than moderate-sized naiads.

An assessment of the temporal aspects of macroinvertebrates associated with *Lagarosiphon* in Lake Kariba was done through a weekly sampling programme that ran from August 2007 to August 2008. A total of 21 macroinvertebrate orders and 50 families were collected. The macroinvertebrate assemblage composition was generally similar throughout the study period. Generally, most taxa were present all year round suggesting multivoltine life history characteristics. Among the common insect taxa total biomass was dominated by coenagrionid naiads and chironomid larvae. The abundances of a number of taxa and total macroinvertebrate abundance were significantly reduced at water temperatures that were greater than $28^{O}C$. High water levels were characterised by significantly greater abundances of some taxa.

The study showed that water temperature, water level fluctuations, differences in plant structural morphology and fish predation are important in structuring epiphytic macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*. It also demonstrated that invertebrate predation may also be an important factor especially in the absence of fish predation. The results are discussed with respect to the management implications of Lake Kariba.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

The sustainable exploitation of ecosystems requires an understanding of ecosystem processes and function (Reynolds 1998). A common goal in freshwater ecology is to understand how communities are structured in space and time, and how biotic and abiotic factors affect their distribution and abundance. The main challenge in attaining this goal is that aquatic ecosystems are complex and the unravelling of biotic and abiotic interactions within these systems can be a bewildering task.

Lake Kariba, which is on the Zambezi River in southern Africa, is one of the large man-made reservoirs in the world. The lake was created in 1958 and in the first decade after its creation it received unprecedented attention on many aspects of its ecology (e.g., Mitchell 1965, 1969, 1970, Bowmaker 1968, 1973, McLachlan 1968). Unfortunately, most were short-term studies and few studies of basic ecological processes have been undertaken over the last two decades. Thus, much remains unknown about the ecology of aquatic communities in Lake Kariba, especially the littoral zone macrophyte and invertebrate communities.

Macrophytes and associated invertebrate assemblages are ecologically important components of freshwater ecosystems (Cheruvelil *et al*. 2000, 2002). The ecological integrity and health of many aquatic systems is dependent upon the availability of healthy macrophyte and invertebrate communities. Thus, studies on macrophytes and invertebrates in rivers, lake and reservoirs are not only of scientific interest, but are important for management and conservation of aquatic resources. This study was therefore initiated so as to understand aspects of the ecology of invertebrates associated with two common and abundant submerged macrophytes, *Lagarosiphon ilicifolius* Obermeyer and *Vallisneria aethiopica* Frenzl in Lake Kariba.

1.2 Aquatic Macrophytes

Aquatic macrophytes are a diverse collection of water based photosynthetic organisms that are large enough to see with the naked eye. They include organisms that are rooted and permanently or periodically submersed below water, or that are rooted but emergent through the water surface, and others that float on the water surface. They therefore, occur in seasonally or permanently wet habitats (Lacoul & Freedman 2006, Chambers *et al.* 2008).

They are seven divisions of aquatic macrophytes. These consist of four macroalgae divisions, the Chlorophyta (green algae, e.g., *Cladophora*), Xanthophyta (yellow-green algae, e.g., *Vaucheria*), Rhodophya (red algae, e.g., *Batrachospermum*) and Cyanobacteria (blue-green algae, e.g., *Oscillatoria*). The other three divisions include the Bryophyta (mosses and liverworts, e.g., *Achrophyllum*), and the two vascular plant divisions, Pteridophyta (ferns, e.g., *Salvinia molesta*, *Azolla*) and Spermatophyta (seed-bearing plants, e.g., *Eichhornia crassipes*, *Lagarosiphon ilicifolius*, *Vallisneria aethiopica*). Most of what is currently known on the species distribution and composition of aquatic macrophytes is on vascular plants. Vascular aquatic macrophytes are represented by 33 orders and 88 families, with about 2,614 species (Chambers *et al.* 2008) and according to Caraco *et al.*, (2006) dominate the shallows of many lakes, rivers, and estuaries

Macrophytes are important to aquatic ecosystems (Blindow *et al*. 2002). They influence the environmental characteristics of water bodies, particularly water chemistry (Heegaard *et al.* 2001, Caraco *et al.* 2006, Kosten *et al.* 2009). They are “hot spots” of metabolism and provide habitat for many other organisms (Jeppesen *et al.* 1998, Caraco *et al.* 2006). Macrophytes, together with phytoplankton (Peckham *et al.* 2006, Hempel *et al.* 2008) and periphyton (Vadeboncoeur *et al.* 2001, 2002) are the major primary producers in freshwater systems and so produce food for aquatic organisms and serve as the base of the food chain (Vadeboncoeur *et al.* 2005, Madsen *et al.* 2008). Macrophytes also affect the interactions among phytoplankton, periphyton, invertebrates and vertebrates (Søndergaard & Moss 1998, Blindow *et al.*

2002). Thus, through their effect on abiotic processes and biotic interactions macrophytes play an important role in aquatic ecosystems.

1.3 Effect of Macrophytes on Water Physiochemical Conditions

Macrophytes are involved in a number of processes that have considerable impact on physicochemical properties of water bodies. These include photosynthesis, biomineralization, transpiration, sedimentation, sediment stabilization, nutrient cycling, materials transformations and release of biogenic trace gases (Carpenter & Lodge 1986, Duarte 1995). In shallow waters, macrophyte beds generally reduce the effect of wind and wave resuspension of bottom materials (Horppila & Nurminen 2001, 2003, Arocena 2007). Macrophytes also tend to reduce water movement, thus reducing the sedimentation rate of suspended material and enabling clear-water states (Scheffer *et al.* 1993, Van den Berg *et al.* 1998). Moderately productive to productive shallow lakes may alternate between two states: a clear state that is largely dominated by macrophytes or a turbid state dominated by phytoplankton (Peckham *et al.* 2006, Kosten *et al.* 2009). In these systems, macrophytes by utilizing and storing nutrients are particularly important in maintaining a clear-water state (Kufel & Kufel 2002, Genkai-Kato & Carpenter 2005, Kosten *et al.* 2009).

Aquatic macrophytes also affect pH, temperature and concentrations of dissolved oxygen. The processes of photosynthesis, respiration and decay can alter concentrations of oxygen, dissolved inorganic carbon and nutrients (Granéli & Solander 1988, Carter *et al*. 1991, Moore *et al.* 1994, Miranda & Hodges 2000, Miranda *et al.* 2000). High density beds of submerged macrophytes usually have low dissolved oxygen concentrations especially at dawn and during die off (Kaenel *et al.* 2000, Miranda & Hodges 2000). According to Frodge *et al.* (1990) dense beds of emergent floating leaved macrophytes tend to cause frequent or persistent low dissolved oxygen conditions within the water column, while Pokorny & Rejmankova (1984) have shown that some floating leaved macrophytes instead of enhancing dissolved oxygen concentration in the water column tend to emit most of their photosynthetically produced oxygen into the atmosphere. By reducing the concentration of dissolved oxygen through respiratory activities or by elevating pH values during intensive photosynthesis macrophytes may also enhance the release of phosphorus from sediments (Granéli & Solander 1988, Barko & James 1998).

Macrophyte decay releases nutrients into the water column (Carpenter 1980, Wilhelm & Doris 1988, Titus & Pagano 2002). Carpenter (1980) suggested that decaying submerged macrophytes in the littoral zone can be a major source of biologically available dissolved total phosphorus and decomposable dissolved organic matter for the pelagic community. Carpenter (1980) went on to suggest that production in the pelagic zone can be greatly enhanced by the decay of macrophytes in the littoral zone. Rooted macrophytes can reduce sediment nutrient stores by using nutrients within sediments (Carignan & Kalff 1980, Barko *et al.* 1988). Rooted macrophytes also provide a link between sediment, water and the atmosphere and so enable the release of biogenic trace gases from sediments and enhancing oxygen penetration into sediments (Pedersen *et al*. 1998). The oxidation of the surface sediment layer through the release of oxygen by shoots and rhizomes may also reduce the rate of phosphorus release from sediments (Barko & James 1998)

Variation in the density of aquatic macrophytes also affects vertical light (Titus & Adams 1979) and temperature (Carpenter & Lodge 1986) gradients. Dense stands of submerged macrophytes may drastically reduce light penetration into the water column (Cattaneo *et al*. 1998). Temperature profiles can also be affected by the presence of dense beds of emergent and emergent floating-leaved macrophytes (Dale & Gillespie 1977). Wilcock & Nagels (2001) recorded wide diurnal variations in pH, dissolved oxygen and temperature in areas of a stream dominated by submerged macrophytes, while under floating macrophytes dissolved oxygen tended to be continually low.

Macrophytes generally increase the surface available for epiphytic microorganisms. In shallow freshwater environments the microbial communities are important in the conversion of nutrients (Mickle & Wetzel 1978a, b). For example, high densities of denitrifying (Eriksson & Weisner 1996, 1997, 1999) and nitrifying bacteria (Eighmy &

Bishop 1989) are normally associated with submersed macrophytes. These populations of microbial communities that occur on submerged surfaces of macrophytes are important for nitrogen metabolism especially in nutrient rich freshwater systems (Eighmy & Bishop 1989, Eriksson & Weisner 1999).

Thus macrophytes can profoundly influence the physical and chemical characteristics of aquatic systems. The impact of macrophytes on the physical and chemical conditions of aquatic ecosystems influences ecological processes as well as the richness, diversity, distribution and abundance of other aquatic organisms.

1.4 Organisms Associated with Aquatic Macrophytes

As has already been mentioned, aquatic macrophytes not only structure the physical and chemical environment in aquatic systems, but also directly and indirectly affect populations of other living organisms. Macrophytes provide substrate, refuge and food for algae, invertebrates and vertebrates. Generally, macrophytes, especially submerged aquatic vegetation, tend to support large densities and diversity of invertebrates (Hedgel & Kriwoken 2001, Free *et al.* 2009), fish (Ye et *al.* 2006) and waterfowl (Noordhuis *et al.* 2002).

1.4.1 Periphyton

Periphyton is the assemblage that consists of autrophic and heterotrophic organisms, including algae, microbes, protozoans and invertebrates, which live on the surfaces of aquatic macrophytes and other substrates. Periphyton plays an important role in primary productivity (Vadeboncoeur *et al*. 2001, 2002, 2005, Liboriussen & Jeppesen 2003, 2009), nutrient dynamics (Wetzel 1993, Vander Zanden & Vadeboncoeur 2002) and food web interactions in aquatic systems (Hecky & Hesslein 1995, Vadeboncoeur *et al*. 2002, 2005). Through the photosynthetic process periphyton producers release oxygen into the aquatic environment and are an important food source for grazing invertebrates and fish (Bronmark 2005). Periphyton may also adversely affect submerged macrophytes through heavy coating, which can prevent light from reaching plant surfaces and so limit plant growth (Liboriussen & Jeppesen 2009) and result in the dominance of phytoplankton (Phillips *et al.* 1978). According to Jones & Sayer (2003) dominance by either submerged plants or phytoplankton in shallow lakes is determined by a trophic cascade, which involves fish, invertebrate grazers and periphyton. They suggest that within the range of nutrients where alternative stable states are possible in shallow lakes, fish are the main determinants of community structure, through a cascading effect of predation on grazing invertebrates influencing the biomass of periphyton and hence, plants (Jones & Sayer 2003).

1.4.2 Vertebrates

Aquatic vegetation plays an important role in structuring fish communities (Rotherham & West 2002, Ye *et al*. 2006). Generally, aquatic vegetation density and biomass have been found to be positively associated with fish species biomass, richness and abundance (Ye *et al.* 2006). The abundance of herbivorous waterfowl has also been shown to be closely related to that of submerged macrophytes (Noordhuis *et al*. 2002, Rybicki & Landwehr 2007).

1.4.3 Epiphytic invertebrates

A variety of criteria based on the mesh size of hand nets have been used to classify the term 'macroinvertebrate.' Most studies have used a mesh size range of between 1 to 5 mm (Jackson 1997, 2003). A mesh size of 0.5 mm has been adapted by the International Standardisation Organisation (ISO) as separation between meio- and macroinvertebrate fauna, a standard that generally includes a number of planktonic copepod and cladoceran species in the macrofauna (ISO 1985). In this study the term 'macroinvertebrate' was defined operationally as those organisms retained by a 0.5 mm mesh.

Macroinvertebrates are essential in the function of aquatic ecosystems (Jackson 2003). They play a vital role in processes such as food web dynamics, productivity, nutrient cycling and decomposition (Wallace & Webster 1996). Macroinvertebrates may be classified into five main functional feeding groups, that is, grazers, shredders, gatherers, filterers and predators, based on morpho-behavioural modes used to acquire food (Cummings 1973, Merrit & Cummings 1996). Grazers feed on periphyton, while shredders feed on decomposing or living plant tissue. Invertebrate collector-gatherers generally subsist on fine particulate organic matter, and filterers primarily sieve fine particulate matter from the water column. Predatory invertebrates mainly feed on other animals, which may include zooplankton, other invertebrates and sometimes vertebrates such as juvenile fish. In food webs, macroinvertebrates generally have an intermediate position between primary producers and higher trophic levels such as fish and so their community composition is influenced by both bottom-up and top-down factors (Wallace & Webster 1996). They are therefore, a critical link between primary producers and upper trophic levels (Kornijów 1997, Crowder *et al.* 1998, Wissinger 1999).

Macroinvertebrates may reside on or within sediments, or may be associated with aquatic vegetation. Although the bottom mud of aquatic ecosystems may seem to be homogeneous and unlikely habitats for high diversity, sediment dwelling or benthic macroinvertebrates are diverse and abundant (Covich *et al.* 1999). Through physical, chemical and biological processes, the seemingly uniform bottom mud substrata are usually heterogeneous entities with numerous distinct niches (Hutchinson 1993), which enables the coexistence of diverse range of macroinvertebrate species. Generally though, epiphytic macroinvertebrates (or those associated with macrophytes) are more diverse and abundant than those associated with bottom mud.

1.5 Factors Structuring Invertebrate Assemblages in Aquatic Ecosystems

A number of factors affect invertebrate assemblages in aquatic ecosystems. These include habitat structure (Kiffney & Roni 2007, Chakona *et al.* 2008), biotic interactions among organisms (Wahlström *et al*. 2000, Benard 2004, Teixeira-De Mello *et al*. 2009), invertebrate life history characteristics (Locklin *et al.* 2006) and water physicochemical conditions (Daufresne *et al*. 2003, 2009).

1.5.1 Effect of habitat structure on aquatic invertebrates

Habitat structure plays an important role in structuring ecological communities and maintaining the integrity of ecosystems. It affects the richness, abundance and biomass of invertebrates (Halaj *et al.* 1998, Chakona *et al.* 2008), fish (Charbonnel *et al.* 2002, Gratwicke & Speight 2005), birds (Raman 2006, Mordecai *et al.* 2009) and mammals (Williams *et al*. 2002, Holland & Bennett 2009).

1.5.1.1 The habitat heterogeneity hypothesis

A core concept in the study of ecology is the 'habitat heterogeneity hypothesis' (MacArthur & Wilson 1967). It suggests that highly complex habitats provide more niches and numerous ways of utilising resources and are therefore associated with greater numbers of species than simple habitats (Tews *et al*. 2004). In essence, greater habitat heterogeneity or complexity increases the abundance and diversity of organisms by providing more living spaces, greater feeding opportunities, enhanced recruitment of young and increased refugia from predation or physical disturbance (Orth 1992). Thus, habitat structure not only determines the number of available niches but also affects biotic processes (e.g. predator-prey interactions) and the impact of environmental factors (e.g. wave action).

1.5.1.2 Aquatic macrophytes and habitat heterogeneity

In most habitats, plant communities determine the physical structure of the environment, and have a substantial influence on the distributions and interactions of animal species (McCoy & Bell 1991, Tews *et al.* 2004). The presence of macrophytes in water bodies generally enhances the complexity of the habitat, and avails a wider range of niches, which sustain more diverse communities than simpler un-vegetated areas (Grenouillet *et al.* 2002). The vegetated areas of aquatic systems are consequently characterised by greater abundance, biomass and diversity of invertebrates (Beckett *et al.* 1992a, Theel *et al.* 2008) and fish (Meschiatti *et al.* 2000, Meerhoff *et al*. 2003, Pelicice & Agostinho 2006, Arend & Bain 2008) compared to un-vegetated sites.

Different species of macrophytes may differ in physical structure, morphology or architecture (e.g. number, size, orientation and arrangement) of leaves, branches and stems (Chick & McIvor 1994). These differences in plant structure contribute to habitat complexity and so affect invertebrate assemblages. Structurally complex macrophytes, such as those with dissected leaves also tend to trap greater amounts of detritus (Sand-Jensen 1998) and provide greater surface area for attachment to periphyton (Cattaneo & Kalff 1980). Periphyton is an important food source for grazing macroinvertebrates and fish. Structural macrophyte complexity is therefore, positively correlated with greater food supply for grazing invertebrates and fish, as well as greater refuge from predators (Pardue & Webb 1985, Rozas & Odum 1988, Diehl & Kornijow 1998, Cheruvelil *et al*. 2000).

Due to technical difficulties in quantifying habitat structure a variety of measures have been used to describe the habitat afforded by macrophytes and contradictory findings have been reported. The measures of macrophyte complexity have included plant growth form or structural morphology (Chick & McIvor 1994), number of plant species (Dionne & Folt 1991), plant biomass (Downing 1986, Cyr & Downing 1988a, Rennie & Jackson 2005), and plant density (Bell & Westoby 1986a, b, Duarte & Kalff 1990). In a study of shallow prairie lakes, Rennie & Jackson (2005) found that invertebrate biomass and total invertebrate densities were positively correlated with macrophyte biomass in lakes. Attril *et al.* (2000) on the other hand found that although there was a significant positive relationship between seagrass biomass with macroinvertebrate richness and abundance, there was no significant increase in complexity with seagrass biomass. They argued that in a bed of seagrass the density and composition of macroinvertebrates is largely determined by the amount of plant but not by plant structural complexity. Cheruvelil *et al.* (2000) showed that macrophytes with finely dissected leaves may support more macroinvertebrates than macrophytes with broader and un-dissected leaves. In contrast, Cyr & Downing (1988a), Brown *et al.* (1988) and Irvin *et al.* (1990) found that macrophytes with dissected leaves did not in general support more invertebrates per unit plant biomass than plant with large leaves. Brown *et al.* (1988) also found greater densities of invertebrates in taxonomically mixed stands of macrophytes than stands with only one macrophyte taxon. Thus, although it is generally accepted that structurally complex macrophyte species are characterised by greater abundance and diversity of aquatic communities the use of different measures to define habitat complexity tends give conflicting results.

1.5.1.3 Habitat heterogeneity and aquatic macrophytes in Lake Kariba

The current study focused on macroinvertebrate assemblages associated with two macrophytes, *Lagarosiphon ilicifolius* and *Vallisneria aethiopica* that are common in the shallow marginal waters of Lake Kariba. The two are morphological different and thus presumably differ in terms of habitat availed to macroinvertebrates. A key aspect of the study was the determination of effect of the differences in morphology of the two macrophytes on plant associated macroinvertebrate assemblages.

1.5.2 Biotic interactions and invertebrate assemblages in aquatic ecosystems

Biological interactions such as predation and competition have a profound effect on aquatic organisms (Dahl & Greenberg 1998, Warfe & Barmuta 2004, 2006). Predation is one of the main factors influencing the population dynamics and community structure of prey species (Sih 1987).

1.5.2.1 Predator-prey interactions

(i) Fish predation

Fish when present are normally the top predators in freshwater bodies and affect the spatial distribution, abundance and body size distributions of invertebrates (e.g., Burks *et al*. 2002). In open pelagic zones of lakes (Carpenter *et al*. 1987) and pools of large rivers (Power 1990) fish predation has strong impacts on invertebrate assemblages. Studies in temperate lakes (e.g., Gliwicz & Pijanowska 1989, Wahlström *et al*. 2000) have shown that fish predation in the pelagic zone usually leads to increase in the density of small individuals or small-bodied species. In vegetated littoral zones of lakes, aquatic macrophytes increase the habitat structural complexity and play a significant role in predator-prey interactions (Jeppesen *et al.*1997). Fish predation efficiency is generally reduced in complex habitats (Nelson & Bonsdorff 1990, Swisher *et al.* 1998) and so in vegetated littoral zones the influence of fish predation is normally reduced (Dibble *et al.* 1996).

In temperate lakes, zooplankton generally move from the pelagic to vegetated margins in the littoral zone during daylight hours in a process that has been termed diel horizontal migration (DHM), so as to escape fish predation in the open pelagic zone (White 1998, Burks *et al.* 2002). Fish predators have also been observed to perform diel migration (Imbrock *et al.* 1996, Järvalt *et al*. 2005) in pursuit of their prey. The presence of vegetation in the littoral zone enhances the chances of zooplankton escaping the fish predators. In the tropics and subtropics a similar response by zooplankton communities to that observed in temperate lakes has not been recorded. This is mainly because in these regions, extremely high numbers of juvenile fish, largely due to multiple or frequent reproduction, and small-bodied species occur among the littoral vegetation and exert strong predation pressure on invertebrates (Iglesias *et al* 2007, Van Leeuwen *et al.* 2007, Teixeira-De Mello *et al*. 2009).

In many freshwater bodies with fish predators, size-selective predation by fish has been shown to reduce the abundance of large-bodied invertebrate taxa, especially the large and mobile invertebrate predators such as most odonate species (e.g., Morin 1984a, b, Blois-Heulin *et al.* 1990, Wellborn *et al.* 1996, Tate & Hershey 2003). A study done in the littoral zone of arctic lakes found that fish greatly impacted macroinvertebrate assemblage by eliminating large invertebrates and reducing species richness, diversity and size distribution of individuals (Tate & Hershey 2003). The same study found that dystiscids and other large invertebrate predators were present in fishless lakes and kept the density of small-bodied invertebrate taxa low. Rennie & Jackson (2005) compared prairie lakes with and without fish and found that the proportion of predatory invertebrate taxa was greater in fishless lakes. In work done in a marsh, Batzer *et al.* (2000) found that epiphytic chironomids were more abundant in the presence of fish predators but decreased drastically in the absence of fish predation. They found that excluding fish resulted in increased populations of chironomid competitors (Plarmobidae and Physidae) and invertebrate chironomid predators (Corixidae and Glossiphoniidae). Thus although fish predation may reduce the abundance of some macroinvertebrate taxa, it may indirectly enable others to flourish. A number of studies have shown that exclusion of predatory fish from aquatic food webs has profound cascading effects on lower trophic levels (e.g., Carpenter *et al.* 1985, 2001, Mancinelli *et al.* 2002). The work by Batzer *et al.* (2000) and Tate & Hershey (2003) illustrated that in fishless water bodies invertebrate predation is an important factor in structuring macroinvertebrate assemblages.

(ii) Invertebrate predation

Macroinvertebrate predators usually feed on other invertebrates (Murdoch *et al.* 1984, Steiner & Roy 2003). In fishless freshwater ecosystems, large predatory macroinvertebrates are generally the top predators, and influence assemblage composition and structure of invertebrates (Benke 1978, Murdoch *et al.* 1984, Arner *et al*. 1998, Steiner & Roy 2003). In the absence of fish predators the overall abundance and number of predatory invertebrate taxa generally increases with increase in habitat complexity (Rennie & Jackson 2005). Odonates because of their size are normally the most important predators (Thorp & Cothran 1984).

Burks *et al.* (2001) assessed the effect of predation by dragonfly naiads (*Epitheca cynosura*) on the cladoceran *Daphnia* in laboratory experiments. They found that regardless of macrophyte presence or architectural complexity the naiads generally eliminated all cladocerans within 24 hours. In field enclosure experiments, Burks *et al*. (2001) found that at low macrophyte densities, damselfly and dragonfly naiads significantly reduced the abundance of *Daphnia*, but the scale of the predatory influence decreased with increasing macrophyte density. They proposed from their results that littoral invertebrate predators may have significant impacts on cladocerans that tend to migrate to littoral vegetation during daylight to escape pelagic predators. In another laboratory experiment, Lombardo (1997) compared the effect of naiads of the damselfly, *Enallagma* sp, in environments of differing habitat complexity on prey species that occurred in its natural habitat. It was found that regardless of the habitat the abundances of the amphipod (*Hyalella azteca*) and turbellaria (*Dugesia tigrina*) were significantly reduced while those of gastropods (*Physa integra* and *Gyraulus parvus*) were not affected.

The impact of multiple predators on prey species depends on a number of factors, including predator-predator interactions (Finke & Denno 2002). Intraguild predation, or the killing and eating of species that use similar, often limiting resources (Polis *et al.* 1989), can reduce the collective impact of predators on prey populations (Finke & Denno 2002). Finke & Denno (2002) showed that in structurally simple vegetation the interaction of salt-marsh-inhabiting invertebrate predators, the mirid *Tytthus vagus* and the wolf spider *Pardosa littoralis*, resulted in reduced abundances of mirids due to predation by spiders, and greater survival of their common prey, the plant-hopper *Prokelisia dolus*. They also showed that structurally complex vegetation habitats reduced the antagonistic interactions between mirids and spiders, which resulted in increased impact on plant-hopper populations. Intraguild predation is common in nature (Arim & Marquet 2004) and has been observed among odonates (e.g., Johansson 1993, Fincke 1994). Although its influence on population level processes is still not fully known the effect of intraguild predation may result in higher densities of the common prey (Rosenhim 1998, Rosenhim *et al.* 1995, Finke & Denno 2002).

Thus predator-prey interactions in aquatic communities can have a variety of outcomes. This is especially so in littoral zone of lakes where the presence of vegetation may provide refuge for some invertebrates from fish predators but expose them to invertebrate predators. Most of the studies on predator-prey interactions of aquatic organisms have been done in temperate regions. Although similarities may occur, differences in life histories of organisms and aquatic community assemblages in tropic and subtropic water bodies compared to those from temperate regions may result in greatly differing outcomes of predator-prey interactions (Iglesias *et al.* 2007, 2008, Jeppesen *et al.* 2007).

1.5.2.2. Other biotic factors

A number of other factors that may influence invertebrate community structure in aquatic ecosystems include competition, allelopathy and life history characteristics of aquatic plants and animals. Although competition has long been recognised as an important mechanism structuring ecological communities (Chase & Leibold 2003), there are few studies that have evaluated the role of interspecific and intraspecific competitive interactions in structuring aquatic invertebrate assemblages. Competition for resources such as food and space is generally high within and between species at high population densities. Some freshwater macrophytes have chemical defences or secondary metabolites to deter herbivores (Kubanek *et al.* 2000, 2001). A number of studies have shown that the abundance and distribution of aquatic herbivores may be affected by the secondary metabolites in the plants (e.g., Bolser *et al.* 1998, Cronin 1998, Cronin *et al.* 2002). In temperate regions a number of aquatic plants have distinct growth cycles that show temporal variation and which affect invertebrate community composition, for example, during the winter period many plant species die and epiphytic invertebrates are restricted to macrophytes adapted to low winter temperatures (Pereyra-Ramos 1981). Seasonal variations in abundances, biomass and production of many invertebrates are influenced by life history characteristics. Most of the studies on freshwater invertebrate life cycles have been done in temperate regions where most invertebrate taxa generally have univoltine (i.e. one generation per year) or bivoltine (two generations per year). In these regions the growth and development of invertebrates is synchronised with seasonal variation in temperature and photoperiod, with growth generally slow in winter and rapid in summer (Brittain & Sartori 2003). In the tropics and subtropics, due to relatively warm temperatures all year round, many freshwater invertebrates exhibit non-seasonal multivotine life cycles (Benke *et al.* 1984).

Thus, a variety of biological factors interact to structure invertebrate communities in freshwater ecosystems and the aquatic macrophytes are a key component of structuring factors. The macrophytes provide myriad of services to epiphytic invertebrate assemblages, which include; refuge from predators, shelter from physical stresses, attachment surfaces for eggs, and food supply in the form of periphyton and plant material. The epiphytic invertebrate assemblages are also strongly affected by abiotic or climatic conditions.

1.5.3 Habitat complexity, predator-prey relations and macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*

An important aspect of the current study was the assessment of predator-prey interactions with respect to variation in morphological structure between *Lagarosiphon* and *Vallisneria*. Studies were conducted to determine the effect of fish predators as well as invertebrate predators on epiphytic macroinvertebrate assemblages. It was hypothesised that increased morphological complexity would result in reduced predation and increased abundance, richness and diversity of macroinvertebrate assemblages.

1.6 Effect of Climatic Conditions on Aquatic Invertebrates

Climate influences a variety of ecological processes and its effects operate through local weather parameters such as temperature, wind, rain, and snow, as well as interactions among these (Stenseth *et al*. 2002).

1.6.1 Temperature: effect on aquatic invertebrates

Invertebrate assemblage structure may change in response to climatic conditions, such as temperature. Temperature has a profound impact on a variety of biological processes from the cellular to the organismal level of organization (Rome *et al.* 1992). In general, temperature increases the metabolic rates of ectotherms (Kruhoffer *et al.* 1987) and has direct effects on growth and development of aquatic organisms (Ward & Stanford 1982, Sweeney & Vannote 1986, Jacobsen *et al.* 1997, Moore & Townsend 1998). The effect of temperature on aquatic ecosystems has become of great interest especially with projected increase in temperatures due to global warming.

Aquatic organisms may be broadly classified as cold stenotherms (with narrow thermal tolerance ranges in cold arctic regions); warm stenotherms (with narrow thermal tolerance ranges in warm regions in the tropics); and eurytherms (with wide thermal tolerance ranges, e.g. in temperate or sub-tropical regions) (Langford 1990). Most studies on the effect of temperatures on aquatic organisms have been done in the northern hemisphere. Generally, in these systems increase in temperatures are likely to lead to some cold stenothermal species being replaced by more eurytopic species (Sweeney & Vannote 1978). In the Upper Rhône River (France), Daufresne *et al*. (2003) showed that an increase in average water temperate of about 1.5^{O}C between the periods 1979–1981 and 1997–1999 resulted in a progressive replacement of coldwater invertebrate taxa by thermophilic invertebrate taxa. Few studies on the effect of temperature variation on aquatic invertebrate assemblages have been undertaken in the tropics and subtropics. According to Dallas (2008) aquatic ecosystems are now seriously threatened by alterations in their thermal regimes through human activities that include heated discharges, flow modifications, riparian vegetation removal and global climate change. Dallas (2008) points out that management of aquatic ecosystems requires greater understanding of thermal conditions and their effects on aquatic organisms.

1.6.1.1 Climate variability hypothesis and aquatic invertebrates

The climate variability hypothesis suggests that in variable temperate climates poikilothermic animals have wide thermal tolerance windows, whereas in constant tropical climates they have small thermal tolerance windows (Compton *et al.* 2007). A number of studies have shown that the upper lethal thermal limits of tropical and subtropical species are closer to maximum habitat temperatures than the upper lethal thermal limits of temperate species (e.g., Addo-Beiako *et al.* 2000, Stillman 2003, Compton *et al.* 2007). This implies that temperate species are better adapted to temperature variation, especially considering the rise in temperatures that may occur due global warming.

According to Stenseth *et al.* (2002) changes in seasonality and mean temperatures may alter predator-prey interactions by changing behaviour, seasonal timing and biomass production. Using microcosm experiments Petchey *et al.* (1999) showed that warmed communities of aquatic microbes mostly lost top predators and herbivores, and became largely dominated by autotrophs and bacterivores. A meta-analysis of the effect of increase in temperatures on aquatic organisms by Daufresne *et al.* (2009) has shown a significant increase in the proportion of small-sized species and young age classes and a decrease in size-at-age. These findings are in agreement with the three rules concerning ecogeographical and ecothermal gradients, the Bergmann's rule, James' rule and Temperature-size rule. According to the Bergmann's rule, warm regions tend to be inhabited by small-sized species (Bergmann 1847 quoted in Daufresne *et al.* 2009); while the James' rule states that, within a species, populations with smaller body size are generally found in warmer environments (James 1970) and the Temperature-size rule states that individual body size of ectotherms tends to decrease with increasing temperature (Atkinson 1994).

Temperature also exerts a strong influence on many physical and chemical characteristics of water, which include vapour pressure, surface tension, density and viscosity, the solubility of oxygen and toxicity of pollutants. The solubility of oxygen in water decreases with increase in water temperature (Kalff 2000, Ficke *et al*. 2007). The metabolic rate of most aquatic organisms also increases with temperature, which generally requires increase in oxygen uptake. Thus temperature may adversely affect a number of aquatic organisms through enhancing their biological oxygen demand whilst indirectly reducing oxygen concentration in water. The sensitivity of invertebrates to chemical pollutants such as copper and zinc generally increases at high temperatures (Cairns *et al.* 1978).

1.6.2 Other physicochemical characteristics and macroinvertebrate assemblages

Water flow is an important aspect for aquatic organisms as it determines the physical habitat in streams and rivers. The life strategies of aquatic invertebrates that evolved in lotic systems are primarily adapted for direct response to the natural flow regimes in these systems. Anthropogenic alterations of flow regimes through building of dams and water abstraction thus have adverse effects on aquatic organisms in rivers and floodplain wetlands (Ward *et al.* 1999, Hart & Finelli 1999). Boulton (2003) found that several groups of macroinvertebrates in two Australian intermittent streams were virtually eliminated by an unusually long drought period despite a return to higher than baseflow conditions. Decrease in water flows may also affect the thermal capacity of a river and result in higher water maxima and lower minima (Webb 1996, Sinokrot & Gulliver 2000) and thus further compound the adverse effects on aquatic organisms.

In lakes and reservoirs periodic fluctuation in water levels also affects macroinvertebrate assemblage structure (Johnson *et al.* 2007). In regulated lakes, too little or too much disturbance from water-level fluctuations has been found to result in reduced structural diversity of the macrophyte and epiphytic invertebrate assemblages (Wilcox & Meeker 1991, 1992, Mastrantuono *et al.* 2008). Reduction in water levels and exposure to the atmosphere causes the death of many aquatic plant species largely through desiccation, and usually results in the death of many invertebrates associated with the plants (McLachlan 1970a, 1974). When water levels are rising aquatic plants generally re-colonise the inundated areas and new macrophyte beds are created. According to Sheldon (1984) and Hargeby (1990) differences in colonization rates of invertebrate taxa are initially the main attributes that structure epiphyitic invertebrate community in new macrophyte beds.

Variations in pH (France 1990), dissolved oxygen (Jacobsen *et al*. 2003, Connolly *et al.* 2004, Kaller & Kelso 2007, Jacobsen & Marin 2008), ammonium and nitrite (Berenzen *et al.* 2001), and generally, variation in water quality can have profound effects on invertebrate assemblages (Emere & Nasiru 2008, Durance & Ormerod 2009). Thus, the physicochemical conditions in aquatic environments are important determinants of invertebrate community assemblages.

1.6.3 Water physicochemical condition and epiphytic macroinvertebrate assemblages in Lake Kariba

The effect of water physical and chemical characteristics on invertebrate assemblages in Lake Kariba, especially littoral zone macroinvertebrates has largely been ignored. The assessment of the response of epiphytic macroinvertebrate assemblages to variation in water physicochemical was a key aspect of the current study. Invertebrate abundance, richness, diversity, biomass as well as a life history characteristics were analysed with respect temporal variation in temperature, water level and other water physicochemical variables.

1.7 Summary

In conclusion therefore, the interactions between water physicochemical characteristics and biological factors affect invertebrates in aquatic ecosystems. The spatial and temporal variations in the environment often result in dramatic fluctuations in the abundance of populations (McCauley 1993). The spatial and temporal heterogeneity of habitats and their related biotic and abiotic fluctuations, together with competitive and prey-predator interactions, fundamentally determine the structure and organization of communities (Thrush 1999). Thus, the epiphytic macroinvertebrate assemblages in freshwater systems are a result of numerous interacting processes. Because of the importance of macroinvertebrates to aquatic ecosystem function it is essential for the management and conservation of freshwater resources to understand the relationship between macrophytes and macroinvertebrates (Cheruvelil *et al.* 2000). To develop theories able to explain community organization and dynamics, it is necessary to detect and describe recurring patterns and to understand the underlying processes (Galuppo 2007).

1.8 Justification of the Study

Lake Kariba was the largest man-made lake when it was formed between 1958 and 1963. It attracted at lot of interest with numerous studies, of both the aquatic and terrestrial environment, undertaken during the first three decades of its existence. Aspects of the ecology of the phytoplankton of Lake Kariba were studied by Thomasson (1965, 1981), MacDonald (1970), Machena (1983), Ramberg (1984, 1987), Ramberg *et al.* (1987), Moyo (1991, 1993) and Phiri *et al.* (2007). Zooplankton studies were conducted by Bowmaker (1973), Begg (1976), Mills (1977), Magadza (1980), Green (1985), Masundire (1989a, b, c, 1991, 1992, 1994, 1997) and Harding

& Rayner (2001). The ecology of aquatic macrophytes received substantial attention from Bowmaker (1968, 1973), Mitchell (1965, 1969, 1970, 1971, 1972, 1973a, b), Machena (1988, 1989), Machena & Kautsky (1988), Machena *et al.* (1990), and Mhlanga (2001). Macroinvertebrate studies were done by McLachlan (1968, 1969a, b, c, d, 1970a, b, 1974), McLachlan & McLachlan (1971), Bowmaker (1973), Mills (1976), Kenmuir (1980, 1981) and Machena & Kautsky (1988). Limnochemistry and fish and fisheries ecology aspects of the lake received much greater attention. A cursory review of literature on Lake Kariba generally shows that as of the late 1990s very little has been done or reported on the ecological aspects of the lake. Generally, there is not much known on the ecology of macrophytes and the associated invertebrates in African lakes and reservoirs.

The littoral zone is an important component of ecosystem dynamics, function and productivity of lakes and reservoirs (Wetzel 2001, Wetzel & Søndergaard 1998, Vakkilainen 2005). Aquatic vegetation in the littoral zone provides habitat for invertebrate fauna (Beckett *et al.* 1992a, b, Cheruvelil *et al.* 2000, 2002) and feeding area for vertebrates such as fish (Diehl & Kornijow 1998, Marklund *et al.* 2002) and birds (Mitchell & Perrow 1998, Marklund 2000, Marklund *et al.* 2002). Aquatic macrophyte beds also serve as spawning ground for several fish species and provide refuge from predators for their fry (Wilcox & Meeker 1992). Change in macrophyte community structure may result in drastic changes in zooplankton (Huusko *et al.* 1988), macroinvertebrate (Palomäki 1994) and fish fauna (Wilcox & Meeker 1992). The conservation and management of aquatic systems requires knowledge of the ecology of aquatic macrophytes and the organisms associated with them. In Lake Kariba, the ecology of macroinvertebrates associated with aquatic plants has received little attention (e.g., Bowmaker 1973, Machena 1988, 1989, Mhlanga & Siziba 2006).

This study therefore was an attempt at understanding some of the aspects that affect epiphytic macroinvertebrate assemblages in Lake Kariba. The original objective was to study the periphyton and macroinvertebrates associated with two of the most common and abundant submerged macrophytes in the lake, *Lagarosiphon ilicifolius* Obermeyer and *Vallisneria aethiopica* Frenzl, so as to develop a biomonitoring framework for shallow marginal waters of the lake. But with little available information on the basic ecology of both periphyton and macroinvertebrate communities of the lake, I realised that an understanding of the ecology of either community was essential before any biomonitoring tool could be developed. I settled on studying macroinvertebrates largely because of prior interest on the use of macroinvertebrates to monitor the health of freshwater systems (see Phiri 2000, Moyo & Phiri 2002).

The study focused on three main aspects; (i) the effect of habitat heterogeneity, (ii) predator-prey interactions, and (iii) water physicochemical conditions on epiphytic macroinvertebrate assemblages in shallow inshore waters of Lake Kariba. On the basis of the habitat heterogeneity concept I hypothesised that:

a. Epiphytic macroinvertebrate assemblages between *Lagarosiphon* and *Vallisneria* would differ due to differences in architectural complexity between the two plants, with greater macroinvertebrate richness, diversity and abundance occurring on *Lagarosiphon* than on *Vallisneria*.
b. Increase in vegetation density cover would result in increased macroinvertebrate richness, diversity and abundance.
c. The effect of fish and invertebrate predation on epiphytic macroinvertebrate assemblages would be greater on *Vallisneria* than on *Lagarosiphon*.

Predators generally tend to have a profound effect on lower tropic levels (Gilinsky 1984, Tolonen *et al.* 2003). Most predators are size-selective and prefer the larger individuals across the range of prey sizes that they are able to consume (Dixon & Baker 1988, Wellborn *et al*. 1996). I therefore hypothesised that:

d. In the absence of fish predators the macroinvertebrate assemblage would be dominated by large and mobile macroinvertebrate predatory taxa that would adversely affect the abundances of small non-predatory invertebrate taxa.
e. In the presence of fish predators the abundance and diversity of large predatory invertebrate taxa would be less than that of small non-predatory taxa due to size-selective fish predation.

f. Large individuals within an invertebrate taxon would be more vulnerable to fish predation than small individuals and for all size-classes the adverse effects of fish predation would increase as fish density increases.

Seasonal variation in climatic conditions has been shown to affect aquatic organisms, with temperature (Stenseth *et al.* 2002, Dallas 2008) and rainfall (Boulton 2003) having significant effects. I therefore hypothesised that:

g. Temporal variation in water physicochemical conditions would affect epiphytic macroinvertebrate assemblages.

1.9 Objectives of the Study

The primary objective of this study was to improve understanding of the ecology of Lake Kariba, especially the aspects of the ecology of epiphytic macroinvertebrate communities. Specifically the study aimed at:

a) Determining whether there were any differences in macroinvertebrate communities associated with the *Lagarosiphon* and *Vallisneria*
b) Assessing the effect of variation in water physicochemical properties on epiphytic macroinvertebrates associated with *Lagarosiphon*
c) Determining seasonal body size distribution, biomass and life history characteristics of the main aquatic insect taxa associated with *Lagarosiphon*
d) Determining the effect of variation in vegetation density cover on macroinvertebrates associated with *Lagarosiphon*
e) Determining the effect of invertebrate and fish predation on macroinvertebrates assemblages associated with *Lagarosiphon* and *Vallisneria*.

1.10 Organization of the Thesis

This chapter gives a general theoretical perspective on freshwater macrophytes and associated macroinvertebrates that has shaped contemporary understanding of the ecology of epiphytic macroinvertebrates in aquatic ecosystems. It also provides justification and objectives of the study. Chapter 2 provides a description of the study area, and a historical background of the development of macrophytes on Lake Kariba. Chapter 2 also dwells on the materials and methods used in carrying out the study as well as in analysing the results. Chapter 3 is a comparative study that reports on the abundance and diversity of epiphytic macroinvertebrate communities associated with *Lagarosiphon* and *Vallisneria*. In Chapters 4, 5 and 6, I concentrate exclusively on macroinvertebrates associated with *Lagarosiphon*. Chapter 4 dwells on seasonal variation of the macroinvertebrate assemblage and the effect of selected water physicochemical parameters. Chapter 5 is a presentation of the results of body size distribution, biomass and life history characteristics of the most common and abundant insect taxa associated with *Lagarosiphon*. In Chapter 6, results of the effect of plant density on epiphytic macroinvertebrate community structure are presented and discussed. Chapters 7 and 8 presents results of experimental work done in ponds to determine the effect of differences, especially in morphological complexity, between *Lagarosiphon* and *Vallisneria*, on aquatic macroinvertebrate assemblage structure. In Chapter 7 I describe the insect assemblage that developed in association with the two submerged plants in the absence of fish predators, while in Chapter 8 I present results of a pilot study on the impact of fish predation on the macroinvertebrates associated with the two plants. In Chapter 9 I present the results of the effect of variation in fish density on damsel naiads associated with *Lagarosiphon*. Chapter 10 provides a general discussion of the study, the implications of its findings, especially with respect to conservation and management of Lake Kariba's aquatic resources, and the study conclusions.

CHAPTER 2

STUDY AREA, MATERIALS AND METHODS

2.1 Introduction

During the 20th century, demands of growing economies after World War II led to a drastic worldwide increase in dam construction. On the African continent the first large dam, Kariba Dam, was created in 1958 by damming the Zambezi River, resulting in the creating of what was then the largest man-made lake in the world, Lake Kariba, between Zambia and Zimbabwe. The lake was created primarily for hydroelectric power generation. The lake is important economically and socially to both Zambia and Zimbabwe. The lake is now a major tourist destination, supports lucrative pelagic and inshore fisheries, and aquaculture (fish and crocodile) industries. The pelagic fish industry is based on a clupeid, *Limnothrissa miodon* (Boulenger, 1906) which was introduced into Lake Kariba from Lake Tanganyika in 1967/1968 (Balon 1971, Bell-Cross & Bell-Cross 1971, Junor & Begg 1971). The basis of the inshore fishery is a range of cichlid species largely comprising of *Oreochromis niloticus*, which was introduced into the lake the 1990s.

2.2 Study Area

2.2.1 Lake Kariba

The damming of the Zambezi River at the Kariba Gorge in December 1958 created what was then the largest man made lake in the world, Lake Kariba (Figure 2.1). The lake reached its maximum retention level in September 1963 (McLachlan & McLachlan 1971). The Zambezi River, with a catchment area of about 1 193 500 km^2, is southern Africa’s largest river and is composed of three ecologically distinct zones, the Upper (1 078 km river length), Middle (853 km) and Lower Zambezi (563 km). Lake Kariba lies within the Middle Zambezi, between latitudes 16^{O}28'S and 18^{O}06'S, and longitudes 26^{O}40'E and 29^{O}03'E. The lake has a surface area of 4364 km^2 at the normal operation level of 484 m a.s.l, a length of 276 km, an average width of 19 km and an average depth of 29 m. The lake's longitudinal axis roughly coincides with the political boundary between Zambia and Zimbabwe and shows a general SW-NE orientation.

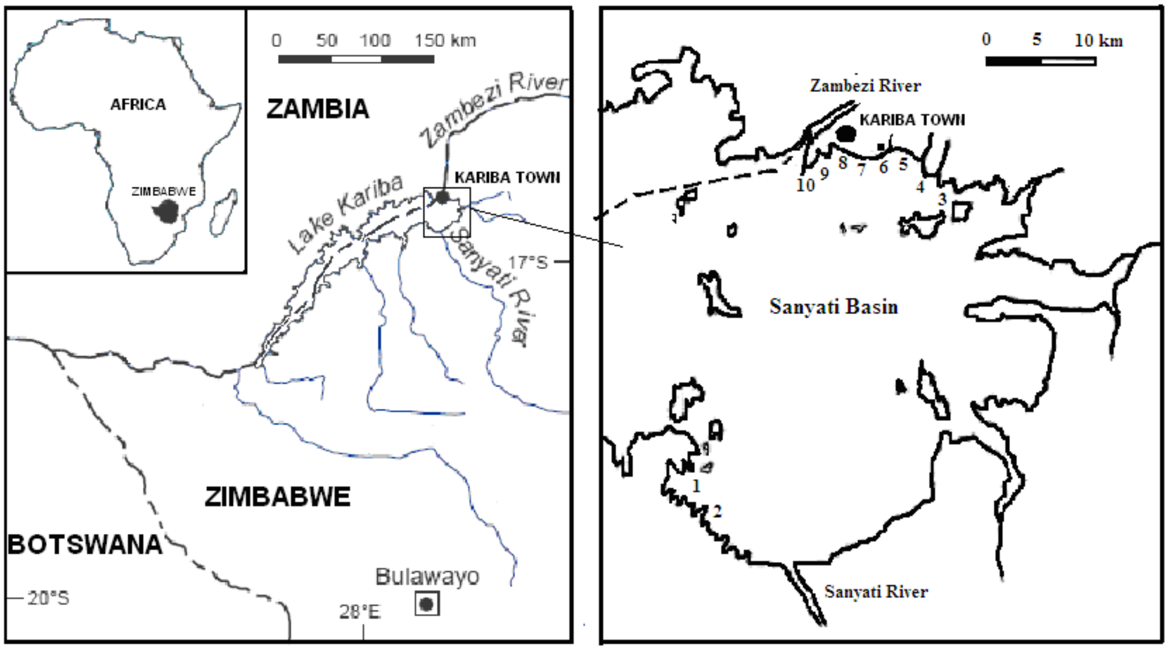

Figure 2.1 **Lake Kariba, showing the locations of the ten sampling station on Sanyati Basin. ■ = Location of the University of Zimbabwe Lake Kariba Research Station.**

Table 2.1 gives a summary of the main morphometric and hydrological characteristics of the lake. Coche (1974) gives a comprehensive review of the physical geography, geology and soils, climate, hydrology, morphometry and morphology, as well as the early limnological aspects of Lake Kariba and the following account is derived from his work, except where other authors are acknowledged.

Table 2.1 Morphometry of Lake Kariba at the normal operating water level (485 m) (Source mainly from Coche 1974; [1] from Mitchell 1973a).

Parameter	
Length	277 km
Mean width	19.4 km
Surface area	5364 km^2
Shore line length	2164 km
Depth (maximum)	93 m
Depth (mean)	29.2 m
Volume	156×10^9 m^3
Renewal time[1]	2.64 years

2.2.2 General climatic conditions in the vicinity of Lake Kariba

The air temperature around Lake Kariba is generally high with mean monthly maximum temperatures consistently over 25^{O}C for much of the year. The hot season occurs between October and March, during which the monthly mean maximum air temperature range is between 29 ^{O}C and 39 ^{O}C, with temperatures above 35^{O}C usually being recorded during October-November. Between April and September, air temperatures are generally lower with mean monthly minimum temperatures below 20^{O}C. The lowest mean monthly minimum temperatures (9 – 10^{O}C) generally occur in June and July. Rainfall around Lake Kariba is highly seasonal, occurring between November and April. There is generally little to no precipitation between May and October. The mean annual rainfall over the lake ranges between 400 – 800 mm.

2.2.3 Hydrological and limnological characteristics of Lake Kariba

The Zambezi River contributes more than 75% of the inflow into Lake Kariba, the remainder coming from secondary rivers, of which the Sanyati and Gwayi which largely flow during the rainy season are the most important. Thus, the Zambezi River has great influence on the hydrological and limnological aspects of the lake. Outflow from the lake occurs mostly through hydroelectric power turbines. In a normal rain season the lake usually experiences a mean drawdown of about 3 m. The water replacement time for Lake Kariba is about 2.6 years (Mitchell 1973a).

Lake Kariba is a phosphorus-limited oligotrophic lake (Magadza 1992). The basin of the lake is largely comprised of nutrient-poor sandstones and so the lake depends on inflows for nutrient supply. The Zambezi River generally has low nutrient levels compared to most African rivers by the time it flows into Lake Kariba. This is because upstream of the lake, the river passes through extensive swamps, the Barotse and Chobe swamp areas, which trap significant amounts of the chemical and silt load of the river (Coche 1974). The lake is monomictic and is stratified from mid August to the end of April; during this period surface water temperatures may exceed 30^{O}C, while bottom water temperatures are normally in the lower 20^{O}Cs. Mixing occurs in winter when temperature throughout whole water column is at about 20 to 22^{O}C.

Lake Kariba has five hydrological basins (Begg 1970, Mitchell 1970) (Appendix 1). The influence of the Zambezi River creates a strong hydrological gradient with productivity and transparency increasing away from the mouth. Basins 1 and 2 have riverine characteristics from November to May, during which period the Zambezi River is at peak flow (Coche 1968). As of July, with decrease in Zambezi River flows and decline in its influence, Basins 1 and 2 assume lacustrine characteristics, with a conventional thermocline at 12 to 15 m (Machena & Kautsky 1988). Basins 3 to 5 are generally lacustrine throughout the year.

The Sanyati basin (Basin 5) is the eastern most basin of Lake Kariba. It makes up about 26% and 23% of the lake’s volume and surface area respectively. The basin receives inflows from the Sanyati River, which is the second largest river draining into Lake Kariba, as well as from the Gache Gache, Nyaodza and Charara rivers.

2.2.4 Aquatic macrophytes of Lake Kariba: a historical account

When the Kariba dam was closed in 1958, the inundation of large amounts of vegetation, other organic and inorganic matter resulted in high productivity in the first five to seven years of existence of Lake Kariba (Balinsky & James 1960, Harding 1966, Petr 1975). The early, eutrophic years of the lake were characterised in many areas by a nearly continuous bloom of blue green algae, dominated by *Microcystis aeruginosa* (Kützing) Lemmermann (Mitchell 1973a), widespread occurrence of a free floating fern *Salvinia molesta* Mitch. (Mitchell 1965, 1969, 1970, 1971, 1972, 1973a, b) and high fish yields (Balon 1974). Productivity gradually decreased as nutrients largely from decaying vegetation were lost through outflow (Harding 1964, 1966) and by the 1970s the lake had become oligotrophic (Mitchell 1973a, Coche 1974).

About forty species of vascular aquatic plants have been recorded in Lake Kariba since its creation. In the initial phases of the lake, high nutrient concentrations and rising water levels favoured the growth and establishment of free-floating macrophytes. The most abundant aquatic plants recorded at the time were *Utricularia inflexa* Forssk. var. *inflexa*, *Pistia stratiotes* L., *S. molesta* and *Lemna* sp. (Balinsky & James 1960, Schelpe 1961). An explosive growth of *Utricularia* spp. in the first few months stopped in October 1959 and by 1961 the plant had become uncommon (Mitchell 1969). The water fern, *S. molesta*, an exotic plant native to south America, then became the dominant aquatic macrophyte, with *P. stratiotes* comprising appreciable though lesser numbers (Balinsky & James 1960, Mitchell 1969). *Salvinia* was initially recorded from the Zambezi River system above the Victoria Falls in 1948 (Mitchell 1969). At its maximum occurrence in May 1962, *Salvinia* covered about 21.5% of the lake's surface (Mitchell 1969). As nutrient levels in the lake decreased, the area covered by *Salvinia* also decreased, and fluctuated between about 10% and 15% from the mid-1960s to the early 1970s (Mitchell 1973b). By 1980, it covered only about 1% of the lake's surface (Marshall & Junor 1981). *Salvinia* now occurs in small quantities on Lake Kariba, and the most dominant and widespread floating aquatic macrophyte is water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach. Although, it is now a common feature on the lake's surface, the coverage of *E. crassipes* has not been as extensive as that achieved by *Salvinia* in the early years of the lake, most probably due to low nutrient levels (Mhlanga 2001).

Two emergent aquatic plants with floating leaves, *Nymphoides indica* (L.) Kuntze and *Nymphaea* sp., occurred in pools that became part of the lake as water levels rose, but these plants did not survive long after inundation (McLachlan 1968) and have generally failed to establish in the lake, likely due to lake level fluctuations. Eighteen emergent macrophyte species have been recorded since the lake was created, including *Phragmites mauritianus* (Kunth), *Typha latifolia* L., *Scirpus cubensis* Poepp. & Kunth, *Ludwigia stolonifera* (Guill. & Perr.) P.H. Raven, *Polygonum senegalense* Meisn. and *Panicum repens* L. The establishment of these species during the initial stages of the lake's development was adversely affected by the *Salvinia* mats. The mats not only made conditions unsuitable for emergent plants to establish themselves within the water column but, according to Magadza (1970), the drying *Salvinia* mats left behind on the shoreline by falling lake levels inhibited the germination of other plants. The decrease in the coverage of the lake surface by *Salvinia* did not result in establishment of permanent stands of the many emergent macrophytes on the shores of the lake due to annual lake level fluctuations which favour species that are able to survive a near-annual cycle of submergence in water as levels rise followed by drying as levels fall. *Panicum repens*, a grass that grows in water and on emergent soils, is widespread and prominent along the lakeshore, because its subsurface stolons enable it to survive periodic desiccation (Magadza1970). Other common emergent plant species include *L. stolonifera* and *P. senegalense*.

The widespread occurrence of *Salvinia* mats in the early years of Lake Kariba, prevented light from reaching much of the lower layers of water and used most of the available nutrients, which resulted in low occurrence of submerged aquatic vegetation (Mitchell 1969). *Ceratophyllum demersum* L. in 1960 (Schelpe 1961), which occurred up to depths of about 10 metres (McLachlan 1968, Donnelly 1968) and *Potamogeton pusillus* L. in 1964 (McLachlan 1968), which grew in water up to a depth of 4 metres, were the first submerged plant species recorded in the lake. *Lagarosiphon ilicifolius* was first recorded in reasonably deep sheltered areas in 1966 (Donnelly 1968). *Vallisneria aethiopica* and *Najas pectinata* (Parl) Magnus were first recorded in 1969 and 1971 respectively (Bowmaker 1973). Machena & Kautsky (1988), in a lake-wide survey, recorded seven submerged macrophyte species, *L. ilicifolius*, *N. pectinata*, *C.*

demersum, *V. aethiopica*, *Potamogeton octandrus* Poir., *Potamogeton schweinfurthii* A. Benn. and *Potamogeton thunbergii* Cham. & Schlecht., with the biomass dominated by *L. ilicifolius* (52%), *N. pectinata* (33%) and *V. aethiopica* (11%). *Lagarosiphon* occurred between 0 and 5 m depth and was present throughout the lake; *Vallisneria* was found to dominate in the western part, basins 1 and 2, largely occurring between 0 and 2 m depth, and was present in small amounts in the other three basins, while *Najas* was largely found in basins 4 and 5, between 0 and 6 m. Machena & Kautsky (1988) also noted that the peak biomasses of *Lagarosiphon*, *Vallisneria* and *Najas* occurred at 1–2m, 1m and 3m depth respectively.

When this study commenced in 2005, *Lagarosiphon* and *Vallisneria* were the most common and widely distributed submerged macrophytes in the shallow marginal waters (depth ≤ 2m) of Sanyati Basin (Basin 5). Although no data are available to confirm qualitative observations, the frequency of occurrence of *Vallisneria* decreased between 2005 and 2008. Other submerged plants that were noted included *C. dermesum*, *N. pectinata*, *P. octandrus*, *P. crispus* and *P. schweinfurthii*, which were less common and occurred in relatively small amounts where present.

2.2.5 Description of *Lagarosiphon* and *Vallisneria*

2.2.5.1 *Lagarosiphon*

Lagarosiphon Harvey (Hydrocharitaceae) is a genus of perennial, freshwater, submerged, aquatic plants consisting of 9 species that are naturally distributed in Africa south of the Sahara, including Madagascar (Symoens & Triest 1983). It is normally rooted, but occasionally may detach and be free floating. Its roots are adventitious and unbranched, and its filiform stems can be as long as 5 m. The stems are circular in transverse section and branching is axillary. Its leaves are sessile, predominantly alternate but may also be subopposite or subverticillate (Symoens & Triest 1983). Although *Lagarosiphon* species are dioecious, reproduction occurs both asexually and sexually. *Lagarosiphon ilicifolius* Oberm. naturally occurs in six southern African countries; the Democratic Republic of Congo, Angola, Namibia, Botswana, Zambia and Zimbabwe. The stems of *L. ilicifolius* are about 3 mm in diameter. The leaves are normally between 2 to 4 mm broad, and 7 to 12mm long (pers. obs.), and are thick and mostly alternate. The leaves may be closely arranged so that the stem and leaves together have a cylindrical outline. The number of leaves per centimetre of stem ranges between 16 and 24 (pers. obs.)

2.2.5.2 *Vallisneria*

Vallisneria L. (Hydrocharitaceae Juss.) has a cosmopolitan distribution (Les *et al.* 2008). Its taxonomic diversity is still in doubt, but it is estimated that there are about four to ten species worldwide (Cook 1996, Les *et al*. 2008). *Vallisneria* species are dioecious, annual or perennial plants. The stem virtually doesn't exist and plants have 6 to 30 (pers. obs.) basally arranged ribbon-like leaves with entire or minutely serrated margins (Russell 1977). *Vallisneria* in Lake Kariba can have leaves with a maximum breadth of about 10 mm. The length of leaves (measured from point of intersection with shoot to the apex) may reach up to about 40cm. The size of *Vallisneria* is generally determined by the physical characteristics of the bottom substrate and wave action Machena (1988). Larger plants generally occur on soft muddy bottoms in protected shores.

2.2.6 Shallow inshore fish community of Lake Kariba

Forty-five fish species have been recorded from Lake Kariba (Marshall 2006) and Zengeya & Marshall (2008) recorded 33 fish species in a lake-wide survey of the inshore fish community. They found that the most abundant species was a cyprinid, *Barbus unitaeniatus*, which comprised 59% of the total number of fish. The Cichlidae, largely comprising *Pseudocrenilabrus philander* (4.6%), *Pharyngochromis acuticeps* (7.8%), *Sargochromis codringtonii* (1.4%), *Serranochromis macrocephalus* (4.2%), *Tilapia rendalli* (6.6%), *Tilapia sparrmanii* (1.3%) and *Oreochromis niloticus* (4.6%), made up 30% of the inshore fish community. A seine-netting survey done between July and December, 2008, as a qualitative assessment of the fish community in shallow waters (depth ≤ 2 m) of a bay on Sanyati Basin (Site 6, Figure 2.1) found that cichlids, mostly *P. philander*, *P. acuticeps*, *T. rendalli*, *T. sparrmanii* and *O. niloticus*, were dominant and generally made up about 70% of the fish assemblage. Generally, greater abundances of fish were associated with aquatic vegetation (pers. obs.).

2.3 Materials and Methods

2.3.1 Invertebrates associated *with* *Lagarosiphon* and *Vallisneria*: effect of plant morphological complexity and water physicochemical properties

Between May and July 2005 ten sites (Figure 2.1) in shallow inshore waters, maximum depth about 1m of Sanyati Basin, were each sampled monthly for selected water physical and chemical variables and epiphytic macroinvertebrates associated with *Lagarosiphon* and *Vallisneria*.

2.3.1.1 Site characterisation

The ten sampling sites were selected in a targeted manner to cover the full range of human activities that are known to occur along the shores of the basin. Each site was qualitatively characterised on the basis of the main human activities and developments occurring within 500 m of the shoreline. The prominent activities and developments generally included residential areas, commercial aquaculture activities, maintenance of boats and boating activities, hotels and other tourist accommodation, roads and vehicles, urban development, industrial development, construction activities, sewage effluent disposal, domestic activities (washing and bathing) and effluent disposal from farming activities. An estimate of the relative degree of human disturbance was obtained by qualitatively scoring the level of impact of each activity or development at each site on a scale of 0 (not occurring at site) through 1 (low) and 2 (medium) to 3 (high). The overall disturbance score obtained for each site was subsequently categorised as belonging to one of four categories; no evident disturbance (0), little disturbance (1–11), moderate disturbance (12–22) and high disturbance (23–33). The site characteristics based on this qualitative scoring of human activities are shown in Appendix 2.

2.3.1.2 Water physical and chemical characteristics

On each of the three sampling dates water samples were collected from each site for the determination of water physicochemical conditions at the sites. Five water samples (2-l bottles) were collected at each site from different points along a stretch of about 100 m. All samples from each site were put into a 20-l bucket from which a 2-l sub-sample was taken for analysis of the concentrations of ammonium (NH_4^+), nitrates (NO_3^-), phosphates (PO_4^-), and total phosphorus (TP). The samples were stored at 4^oC and the analyses were done within 48 hours of collection. Water temperature (^OC), pH, dissolved oxygen (DO), conductivity ($\mu S\ cm^{-1}$) and turbidity (NTU) were measured in situ. Temperature was measured using a mercury thermometer, and pH was measured using a WTW 330i (Geotech Environmental Equipment, Denver, Colo. USA) pH meter, calibrated using two-stage calibration against buffers at pH 7 and 9. Conductivity was determined by using a WTW Cond 330i conductivity meter (Geotech Environmental Equipment, Denver, Colo. USA) and reported at 25^OC. Turbidity was measured with a Hach Field Turbidimeter after calibration with standards of 10 NTU and 100 NTU and dissolved oxygen was measured with a WTW Oxi 330 oxygen (Geotech Environmental Equipment, Denver, Colo. USA) meter that was calibrated in water vapour-saturated air using the OxiCal®-SL calibration vessel.

The concentrations of total phosphorus (TP), phosphates (PO_4^-), total nitrogen (TN), ammonium (NH_4^+), and nitrates (NO_3^-) were measured using spectrophotometric methods as described by Bartram & Ballance (1996). Spectrophotometric determination following decomposition by acid and total hydrolysis to hydrogen phosphate ions was used to determine total phosphorus concentration (i.e., total organic & inorganic phosphorus plus the total dissolved phosphorus). Orthophosphate concentration was determined as a molybdophosphate complex (phosphorous molybdenum blue) by using ammonium molybdate to convert the hydrogen phosphate ions to ammonium molybdophosphate, which was then extracted with a benze/isobutyl alcohol mixture and reduced in the organic phase with tin acid tin (II) chloride solution to phosphorus molybdenum blue. Ammonium concentration was determined using the indophenol blue method. The cadmium reduction method was used to determine nitrate concentrations.

2.3.1.3 Epiphytic invertebrates

At each site, for both *Lagarosiphon* and *Vallisneria*, five to seven monospecific patches were randomly chosen from different points along a stretch of 100 – 200 m and plants collected for sampling of epiphytic macroinvertebrates. Only those patches that were at least 1 m^2 in size and had more than 5 individual plants randomly scattered within a 1 m^2 segment were sampled. The minimum distance between any two patches sampled was about 2m.

A square-framed (0.25 by 0.25 m) hand net with a 500 µm mesh and a detachable sample collection bottle was used to sample for epiphytic macroinvertebrates. The net was put alongside the plants while ensuring minimum disturbance. Using scissors at least three plants were cut at the base, placed into the net and brought out of the water. The plants were kept within the sweep net as they were thoroughly washed in a bucket containing water. The macroinvertebrates washed into the detachable bottle were transferred to a sample bottle and preserved in 70% ethanol for taxonomic analysis and enumeration in the laboratory. The washed plant material was collected into labelled plastic bags, stored in cooler boxes and later dried at 105^{O}C for 24 hours to determine dry mass. Identification of macroinvertebrates was based on Edmondson (1959), Day *et al.* (1999, 2001a, b, 2003), Day & de Moor (2002a, b) and de Moor *et al*. (2003a, b). The macroinvertebrates were identified to generic level except for taxonomically challenging groups such as the Oligochaeta, Hydracarina, Cyclopoida, Ostracoda, and most of the Dipteran larvae. The macroinvertebrates were also categorised into primary feeding groups according to Merrit & Cummings (1996), so as to assess the feeding dynamics of the invertebrates associated with the two macrophyte species.

To test for the effect of differences in macrophyte complexity on body size distribution of macroinvertebrates the body lengths of sample specimens of *Cloeon* and damselflies of the family Coenagrionidae (*Pseudagrion*, *Enallagma* and *Ischnura*), as well as head widths of chironomid larvae were measured using a dissecting microscope fitted with a calibrated graticule.

2.3.1.4 Data analysis

Before analysing for any differences among sites or between the two plants, data were tested for normality and homogeneity of variance using Shapiro-Wilks normality test and the variance ratio F test respectively (Sokal & Rohlf 1981). Parametric tests were used to test for differences in instances when the data were normal and variances homogeneous. When the data were not normal and variances were non-homogeneous, and transformation using either log n or log (n + 1) did not normalize the data, non parametric test were used to test for differences.

Macroinvertebrate abundance was standardised by plant dry weight and abundances expressed as numbers of animals per gram of plant dry mass. For each sample the number of taxa (richness) was recorded and Shannon-Wiener (H') diversity indices were obtained using the PRIMER-e version 6.1.5 (Clarke & Gorley 2006) software package. Analysis of variance (ANOVA) was used to test for differences among sites in physical and chemical variables, vegetation dry mass, invertebrate taxa richness, diversity and total invertebrate abundance. The statistical differences in macroinvertebrate assemblage between the two macrophyte species were assessed using the Wilcoxon signed-rank paired samples test. Spearman rank correlation analysis was used to explore the relationships between water physicochemical variables and the macroinvertebrate assemblage structure. The Kolmogorov-Smirnov 2-sample test was used to test for differences in size structure distributions of macroinvertebrates associated with the two macrophytes. The statistical package Simfit version 6.0.24 (Bardsley 2009) was used for statistical analysis of the data.

Non-parametric multivariate analyses were also used in analysing the data for differences in epiphytic macroinvertebrate structure of the two submerged plant species using PRIMER-e version 6.1.5 (Clarke & Gorley 2006). Assemblage patterns were visualised in reduced dimensional space using non-metric multidimensional scaling (nMDS). Analysis of similarities (ANOSIM) was used to test for differences in macroinvertebrate community structure. The similarities percentages procedure in SIMPER was used to ascertain the taxa responsible for similarities and dissimilarities between samples.

2.3.2 Temporal variation and the effect of selected water physical and chemical parameters on macroinvertebrates associated with *Lagarosiphon*

This study was carried out from August 2007 to August 2008 at a site in Basin 5 of the lake (Site 6, Figure 2.1). Water samples for analysis of selected physical and chemical variables and epiphytic macroinvertebrates samples were collected weekly along a stretch of about 500m of the shoreline of the lake. The shoreline from which the samples were collected consisted of a section that was sheltered, one moderately exposed and another fully exposed to wave action.

2.3.2.1 Water physical and chemical characteristics

The water temperature (^{O}C), pH, conductivity ($\mu S\ cm^{-1}$), turbidity (NTU) and dissolved oxygen concentration (%saturation) was measured in situ at three zones, sheltered, moderately exposed and fully exposed to wave action , of a stretch of about 500m of the shoreline. The meters used in measuring temperature, pH, conductivity, turbidity, dissolved oxygen are described in section 2.3.1.2. These measurements were taken weekly for most of the thirteen-month sampling period. Lake level data were obtained from the Zambezi River Authority (ZRA).

Water samples were also collected from areas sheltered, moderately exposed and fully exposed to wave action, for measurement of total phosphorus (TP), phosphates (PO_4^{3-}), total nitrogen (TN), ammonium (NH_4^+) and nitrates (NO_3^-) using spectrophotometric methods as described by Bartram & Ballance (1996) (see section 2.3.1.2 for description of methods used in measuring TP, PO_4^-, NH_4^+ and NO_3^-). The Kjeldahl's decomposition method was used to determine total nitrogen. The concentrations of total phosphorus, phosphates, total nitrogen, ammonium and nitrates were measured from August 2007 up to April 2008.

2.3.2.2 Macroinvertebrate community structure

Epiphytic invertebrates associated with *Lagarosiphon* were collected nearly weekly over the thirteen-month sampling period. Each macroinvertebrate sample consisted of a composite obtained from the sheltered, moderately and fully exposed zones of the shoreline, by randomly sampling fifteen to twenty plants of *Lagarosiphon* from each segment. The samples were collected using a sweep net with a 500μm mesh, and vegetation and macroinvertebrates processed as described in section 2.3.1.3. The macroinvertebrates collected were preserved in 10% formalin.

2.3.2.3 Data analysis

The statistical differences in water temperature, pH, conductivity, turbidity, and in concentrations of ammonium and nitrates among months were assessed using nonparametric Kruskal-Wallis Analysis of Variance (ANOVA), with the Mann Whitney U test used for pair-wise comparisons of differences between months. Assessment of differences in the concentrations of dissolved oxygen (DO) and total phosphorus (TP) among months was done using Analysis of Variance (ANOVA) and the Tukey Q multiple comparisons test was used for pair-wise comparison of differences between months. Temporal patterns in water physicochemical parameters were also explored using principal components analysis in PRIMER-e version 6.1.5 (Clarke & Gorley 2006).

Macroinvertebrate abundance was standardized by plant dry weight and expressed as numbers of animals per gram of plant dry mass. The temporal differences in the total overall abundance of macroinvertebrates and the detailed analyses of the temporal differences in abundance of the most common taxa (those that occurred in 30% or more of the total number of samples) was explored using ANOVA. Three univariate community assemblage measures were calculated for each sample, the number of taxa (S), Pielou's (J) evenness index and Shannon-Wiener (H′) diversity index using the PRIMER-e version 6.1.5 (Clarke & Gorley 2006) and their temporal differences explored using ANOVA. The relationships that the most common macroinvertebrate taxa and univariate measures of community structure had with water chemical parameters were determined using Spearman rank correlation analysis. Statistical analyses were done using the Simfit statistical software package version 6.0.24 (Bardsley 2009).

Non-parametric multivariate analyses were also used to investigate the temporal differences in macroinvertebrate structure between months using the PRIMER-e version 6.1.5 (Clarke & Gorley 2006). Assemblage patterns were visualised in reduced dimensional space using non-metric multidimensional scaling (nMDS). Analysis of similarities (ANOSIM) was used to test for differences in macroinvertebrate community structure between months. The similarities percentages procedure in SIMPER was used to expose which taxa were responsible for the similarities within samples collected in the same month as well as which taxa were responsible for dissimilarities between different months.

2.3.3 Body size distribution, biomass estimates and life histories of common insect taxa associated with *Lagarosiphon*

2.3.3.1 Insect body-size measurement and estimation of biomass

The body sizes of sample specimens of the most common and abundant insect taxa associated with *Lagarosiphon* and collected over a thirteen-month period (section 2.3.2) were measured. The total body length (excluding antennae and cerci) of *Caenis* sp., *Cloeon* sp., Coenagrionidae, *Micronecta* sp. and the head width of Chironominae and Orthocladiinae were measured using a dissecting microscope fitted with a calibrated graticule. Biomass (mg dry mass) was estimated for individual taxa by using length–mass regressions obtained from Benke *et al.* (1999) (Table 2.3). Mean larval size for each week was multiplied by abundance to obtain total biomass per sample of vegetation. The biomass of each insect taxon was expressed in mg per gram of vegetation dry mass.

Table 2.3 Mean values of *a* and b for the body size-mass equations (DM = *a* L^b or DM = *a* HW^b) used to obtain estimates of insect biomass. DM is dry mass in mg, L is total body length in mm, HW is head width in mm and *a* and *b* are constants. (Source: Benke *et al.* 1999)

Family	Taxon	*a*	*b*
Baetidae	*Cloeon* spp.[1]	0.0053	2.875
Caenidae	*Caenis* spp.[1]	0.0054	2.772
Coenagrionidae	Coenagrionidae	0.0051	2.785
Corixidae	*Micronecta* spp.[1]	0.0031	2.904
Chironomidae	Chironominae[2]	1.9574	2.589
Chironomidae	Orthocladiinae[2]	1.7899	2.311

[1]Used family level values of *a* and *b*; [2]Dry mass based on head width (HW) measurements of larvae

2.3.3.2 Data analysis

Body-size frequency distribution graphs were used to explore basic life history patterns of the insect taxa. Temporal differences in the body size-frequency distribution of each taxon were assessed using the Kolmogorov-Smirnov test. The temporal variation in the biomass of each taxon, overall insect biomass and differences in the biomass between different taxa were analysed using analysis of variance. Spearman rank correlation analysis was used to explore the relations between insect biomass and water physicochemical variables.

2.3.4 Effect of plant density on macroinvertebrates associated with *Lagarosiphon*

2.3.4.1 Measurement and characterisation of vegetation density

The study was carried out in the hot dry season, September and October 2008. Over a period of three weeks, samples were collected weekly from the shallow waters (0.5m to 1m) of a bay close to the University of Zimbabwe Lake Kariba Research Station (Site 6, Figure 2.1). During the study period the submerged vegetation in the bay was largely comprised of monospecific patches and beds of *Lagarosiphon*. There were also some few patches of the floating macrophyte, *E. crassipes*. During each sampling date a qualitative method was used to categorise *Lagarosiphon* into low-, moderate- and high-density beds. Low-density beds were those comprising of at most five individual plants randomly scattered within an area of 1m^2. Patches in which the individual plants were virtually uniformly distributed within 1m^2 but with much of the bottom of the lake visible from above were classified as moderate density beds. High-density beds were those in which the vegetation cover within a 1m^2 segment was such that the bottom of the lake was completely covered and not visible from above.

2.3.4.2 Water physicochemical assessment

During each sampling date three patches for each vegetation density category were identified. A distance of at least 5m was maintained between beds of different density categories, while that between the two patches of the same density category was between 3 and 5m. Two vegetation beds of the same density category were randomly selected and temperature, pH, conductivity and dissolved oxygen measured at mid depth in the centre of the each bed, while epiphytic macroinvertebrates were sampled from the third patch. Temperature, pH, conductivity and dissolved oxygen were measured with a mercury thermometer, a WTW 330i pH meter (Geotech Environmental Equipment, Denver, Colo.) and WTW Oxi 330 oxygen meter (Geotech Environmental Equipment), respectively (see section 2.3.1.2).

2.3.4.3 Macroinvertebrate sampling

In sampling and processing epiphytic macroinvertebrates, a sweep net with a 500µm mesh was used as described in section 2.3.1.3. All the plants within the low-density patches were sampled while in the moderate and high-density patches a handful of some of the plants from the centre of the beds was sampled. The collected invertebrate samples were preserved in 10% formalin. The body lengths of *Cloeon* sp. and damselflies of the family Coenagrionidae (*Pseudagrion*, *Enallagma* and *Ischnura*) were measured using a dissecting microscope fitted with a calibrated graticule to determine whether vegetation cover affected size-class distribution of the insect taxa.

2.3.4.4 Data analysis

All statistical tests were done using the Simfit statistical package (Bardsley 2009). One-way analysis of variance (ANOVA) was used to analyse for differences that the three density categories had in water physical conditions and in the vegetation dry mass collected from each category.

Macroinvertebrate abundance was standardized by plant dry weight and abundances expressed as numbers of animals per gram of plant dry mass. Before analysing the macroinvertebrate data the total abundance and abundances of individual taxa were $\log_{10}$ (x+1) to normalize distributions and homogenize variance among factors. Shannon-Wiener (H′) diversity for each sample was obtained using the PRIMER-e version 6.1.5 (Clarke & Gorley 2006). Differences in total abundance, species richness (number of taxa) and the diversity among the three vegetation density groupings were analysed using one-way analysis of variance (ANOVA). Non metric multidimensional scaling (nMDS) and analysis of similarities (ANOSIM) were also used to explore for differences in macroinvertebrate structure among the three vegetation density categories.

Variation in the abundances of functional feeding groups among the weed bed densities was assessed using analysis of variance. The Kolmogorov–Smirnov test was used to test for differences in body size class distribution of *Cloeon* and Coenagrionidae in the three vegetation density categories.

2.3.5 Aquatic insects associated with *Lagarosiphon* and *Vallisneria* in fishless ponds

2.3.5.1 Description of ponds

The study comprised six small artificial ponds at the University of Zimbabwe Lake Kariba Research Station. The circular ponds with a diameter of 2.2 m and a depth range of between 0.7 and 0.9 m are made of iron sheeting. The bottom substrate of the ponds comprised a mixture of sand and mud obtained from the shores of Lake Kariba. Every fortnight the ponds were filled to overflowing with tap water that originated from the lake and had been treated using sand filtration and chlorination by the municipality of Kariba.

2.3.5.2 Culture and maintenance of plants in ponds

Lagarosiphon and *Vallisneria* were collected from Lake Kariba for culture in the ponds. Before planting, the plants were thoroughly washed using tap water to remove invertebrates that were on them while in the lake. Using random selection, two ponds were cultivated with *Vallisneria*, another two with *Lagarosiphon*, and the remaining with a mixture of the two plant species. An attempt was made to ensure that as much as was possible of the bottom substrate of each pond was covered by vegetation. The ponds cultured with both plants were divided into two equal parts; one side cultivated with *Vallisneria* and the other with *Lagarosiphon* and were regularly maintained to ensure there was no complete mixing in the growth of the two plants. The ponds were created and aquatic vegetation grown in August/September 2007. There were maintained for ten months while aquatic insects colonised and became established in each pond.

2.3.5.3 Macroinvertebrate sampling and processing

Over a period of six weeks, July to August 2008, macroinvertebrate samples associated with the plants were collected every two weeks from each pond using a square-shaped (0.25 by 0.25 m) sweep net with a 500 μm mesh. In the monoculture ponds, sampling for insects involved sweeping over two approximately 1 m long stretches of vegetation, while in the ponds with both plant species an approximately 1 m stretch of each plant was sampled. Macroinvertebrate specimens were sorted from the vegetation, preserved in 10% formalin, and later identified to the lowest possible taxonomic level. Length measurements of major group of insects were done using a dissecting microscope with a calibrated graticule.

2.3.5.4 Water physicochemical assessment

Water physicochemical characteristics, temperature (^{O}C), pH, conductivity (μS cm^{-1}) (mgL^{-1}), and dissolved oxygen (DO) concentration (mgL^{-1}) of each pond were recorded on a weekly basis using the appropriate meters (see section 2.3.1.2).

2.3.5.5 Data analysis

The design employed in this experiment consisted of two replicates per treatment. According to Carpenter (1990), inadequate replication as was used here, may be worse than no replication at all since variability of community and ecosystem variates can be quite high, such that treatment effects are not detected unless they are very large. The samples that were collected every fortnight from each pond over the six week period were pseudoreplicates (see Hulbert 1984). I therefore did not use inferential statistics to compare the macroinvertebrate assemblages among ponds and between the two macrophyte species.

The exploration of differences in water physiochemical characteristics among ponds was done using principal components analysis (PCA) and cluster analysis. Macroinvertebrate abundance was expressed as number of animals per sweep. The non-metric multidimensional scaling (nMDS), analysis of similarities (ANOSIM) and the similarities percentages (SIMPER) procedures were used to explore for similarities and differences in insect community structure between *Lagarosiphon* and *Vallisneria*. Two univariate community assemblage measures were also calculated for each sample, the number of taxa and Shannon-Wiener (H′) diversity index using the PRIMER-e version 6.1.5 (Clarke & Gorley 2006) and used to assess the differences in insect community assemblage associated with the two macrophyte species. The Kolmogorov –Smirnov test was used to test for differences in body size class distribution of insects associated with the two plants when they grew in separate ponds as well as when they were grown in the same pond. Statistical analysis was done using the Simfit statistical software package version 6.0.24 (Bardsley 2009).

2.3.6 The effect of fish predation on macroinvertebrates associated with *Lagarosiphon* and *Vallisneria*: a pilot study in small ponds

This study was carried out in three circular ponds (dimensions of ponds described in section 2.3.5). In Pond 1, *Vallisneria* grew as the only plant, and in Pond 2 *Lagarosiphon* was the sole plant. Pond 3 contained the two plants, which were maintained as separate stands in two halves of the pond. This experimental system was initially set up in February 2009. Sampling for macroinvertebrates associated with the plants (see section 2.3.5 for sampling method) in three ponds commended on the 18th of June 2009 and ended on 30 August 2009. From 18 June to 14 July the ponds were sampled on three separate occasions in a fishless state. On 16 July twenty juvenile cichlid fish were added to each pond, which resulted in a density of 5 fish per m^2 of bottom surface area of each pond. The fish consisted of a mixture of *Orechromis niloticus, Tilapia rendalli* and *Tilapia sparrmanii* and had a total body length size class range of between 4 cm to 10 cm. The fish were collected by seining in shallow inshore waters (Site 6, Figure 2.1) of Lake Kariba in April/May 2009. After fish were added, Ponds 1 and 2 were sampled weekly on six separate occasions from 23 July to 30 August, while Pond 3 was sampled five times.

The abundances of different macroinvertebrate taxa associated with the plants in each pond were analysed before as well as after fish were added to the ponds. The experimental design had no replicates with the repeated samples taken from each pond being pseudoreplicates (see Hulbert 1984). Therefore, it was not appropriate to use inferential statistics for the determination of the effect of fish predation on invertebrate abundances. I explored the percent changes in abundances to assess fish predation effects. The effect of fish predation on size class distribution of coenagrionid and libellud naiads, and chironomid larvae was also determined (see section 2.3.3.1 for measurement of body size dimensions) and the data analysed using the Kolmogorov-Smirnov test.

2.3.7. An assessment of short-term survivorship of *Ischnura* (Odonata: Coenagrionidae) naiads at different densities of juvenile *Oreochromis niloticus*

In this study, eleven glass aquaria were used, eight of which were small with dimensions of 0.25 m length, 0.25 m width and 0.25 m height. The other three aquaria were larger and had a length, width and height of 0.5 m, 0.4 m and 0.3 m respectively. The bottom surface areas of the small and large aquaria were 0.0625 m^2 and 0.2 m^2 respectively.

2.3.7.1 Vegetation density

Lagarosiphon was collected from Lake Kariba (Site 6, Figure 2.1) and thoroughly but carefully washed using tap water to remove attached invertebrates. Healthy (i.e. green with no chlorotic parts) stems were selected and 12 cm segments of the apical section of each stem obtained. The bottom 2 cm of each 12 cm segment was inserted into a hollow central part of a lead weight so that in the aquaria 10-cm-long fronds stood upright in filtered water. In each of the eight small aquaria 36 plants were randomly added and covered much of the bottom surface, while in the three larger aquaria 115 plants were added. Thus stem density in the small and large aquaria was 576 and 575 stems per m^2 of bottom surface respectively. The vegetation density cover in the aquaria was generally equivalent to the moderate-density category as described in section 2.3.4.1. Upon completing the experiment, samples of stems from each aquarium were collected and the number of leaves counted so as to determine whether leaf density differed among aquaria. The water level in all aquaria was at 12 cm, which meant that 7.5 and 24 litres of water were added to small and large aquaria respectively. The water used was collected from fishless ponds (section 2.3.5) and was filtered through a 75 μm mesh. The aquaria were aerated throughout the study period.

2.3.7.2 *Ischnura* naiad size classes and density

The *Ischnura* naiads used in the experiment were collected by sampling *Lagarosiphon* beds at site 6 (Figures 1). The naiads were separated into three size class categories, small-sized (< 5 mm), moderate-sized (5 mm < length < 10 mm) and large-sized naiads (> 10 mm). The lengths of naiads were measured from the front tip of the head to the tip of the last abdominal segment. Only naiads with all three caudal appendages were selected.

Twenty small- and moderated-sized naiads were added into all the eight small aquaria, while 64 small- and moderate-sized naiads were added in the three larger aquaria. Thus, the density of both small- and moderate-sized naiads was 320 per m^2 in all eleven aquaria. Relatively low numbers of large-sized naiads were obtained compared to small- and moderate-sized naiads, so that 10 and 20 large-sized naiads were added into each of the eight small and three larger aquaria respectively. Thus, the density of large-sized naiads was 160 per m^2 and 100 per m^2 in small and larger aquaria respectively. The *Ischnura* naiads were added to the aquaria at between 8 and 10 am, immediately after being collected from the lake, and kept in the aquaria for at least two hours before fish were added.

2.3.7.3 Fish (*Oreochromis niloticus*) densities

Juveniles of *Oreochromis niloticus* (total length range 2.8 – 4.6 cm) were collected by seining in shallow inshore waters (Site 6, Figure 2.1) of Lake Kariba five days before *Ischnura* naiads were added to aquaria. The fish were kept in a storage glass aquarium, which was 3 m long, 0.75 m wide and 0.75 m high. On the second and third day after being caught, the fish were fed twice on each day, at about 9 am and 3 pm on a mixture of live invertebrates including coenagrionid naiads, which were obtained from *Lagarosiphon* beds in Lake Kariba. On the fourth day, that is a day before being added to the experimental aquaria, the fish were not fed.

The fish were added into the experimental aquaria at least two hours after the *Ischnura* naiads in the following densities: 0, 32, 64 and 255 per m^2 of bottom surface of the aquaria. The treatment without fish had two replicates in small aquaria, while three replicates were performed for the other 3 fish densities. The three replicates of the highest fish density were performed in the three larger aquaria. The fish were added to aquaria at between 12 midday and 2 pm.

2.3.7.4 Recording naiad survival

After 24 hours the plants were carefully removed from the aquaria and each plant thoroughly washed in a white tray so as to dislodge the attached naiads. After having removed the fish, the water in each aquarium was inspected to check for naiads that may have been overlooked or dislodged into the aquarium during removal of plants. The number and sizes of naiads collected from each aquarium were counted and recorded as dead or alive. The naiads were then preserved in 70% ethanol and later examined under a dissecting microscope fitted with a calibrated graticule to confirm the taxonomy and body length of each specimen.

2.3.7.5 Data analysis

Analysis of variance (ANOVA) was used to determine whether there were differences in leaf density among aquaria. ANOVA was also used to assess, (i) whether the mean percent survivorship of each naiad size class was significantly different among the four fish densities and (ii) whether there were differences in percent survivorship among naiad size classes at each of the four fish densities.

CHAPTER 3

INVERTEBRATES ASSOCIATED WITH *Lagarosiphon* AND *Vallisneria*: EFFECT OF PLANT MORPHOLOGICAL COMPLEXITY AND WATER PHYSICOCHEMICAL PROPERTIES

3.1 Introduction

The abundance and diversity of epiphytic macroinvertebrates is affected by macrophyte abundance, structure and community composition (Cheruvelil *et al.* 2002). Epiphytic macroinvertebrate abundances tend to be greater on plants with complex than those with simply morphologies (Cheruvelil *et al.* 2000, 2002), because morphologically complex plants have more attachment and better refuge sites than morphologically simple plants (Thomaz *et al.* 2008). Thus plants with finely dissected leaves generally have higher invertebrate abundance per unit biomass than broad-leaved plants (Rooke 1986a, b, Chilton 1990).

Lagarosiphon ilicifolius and *Vallisneria aethiopica* are structurally different submerged macrophytes, common and abundant in shallow marginal areas of Lake Kariba. *Lagarosiphon* is morphologically more complex than *Vallisneria*. Both plants are important habitats and sources of food for a number of organisms. *Lagarosiphon* spp. offer a substrate for a great variety of invertebrates and are eaten by some water birds (Symoens & Triest 1983). A number of species of water birds (Schloesser & Manny 1990, Knapton & Petrie 1999, Zhang & Lu 1999), and freshwater crabs, herbivorous fish and turtles (Zu *et al.* 1999, Armstrong & Booth 2005) are known to feed on *Vallisneria* spp. According to Schloesser & Manny (1990), a decrease in numbers of some migratory waterfowl in the Detroit River (USA) between 1950 and 1985 was due to decrease in the densities of American wildcelery (*Vallisneria americana*) in the river. A study of the diets of six species of migrating water birds on Lake Erie (USA) by Knapton & Petrie (1999) found that out of twenty-nine submerged macrophytes, *V. americana* was the most common food item. In the Fwa River, a river in the Democratic Republic of the Congo (DRC), *V. aethiopica* is the most dominant submerged macrophyte and the most important food item for two endemic cichlid fish species *Thoracochromis callichromus* and *Thoracochromis brauschi* (Roberts & Kullander 1994). In an experimental study, Chifamba (1990) showed that when offered a selection of four submerged plants (*Ceratophyllum demersum*, *L. ilicifolius*, *Najas pectinata* and *V. aethiopica*) juveniles of the red breasted cichlid, *Tilapia rendalli*, primarily fed on *Vallisneria*. According to Feldman (2001) the leaves of *Vallisneria* may support large numbers of invertebrates.

The purpose of this study was to determine whether epiphytic macroinvertebrate abundance, composition and diversity differed between *Lagarosiphon* and *Vallisneria*. The hypothesis tested was that the greater morphological complexity of *Lagarosiphon* would result in greater macroinvertebrate abundance and diversity, and a different macroinvertebrate composition to that associated with the morphologically less complex *Vallisneria*. Habitat structural complexity also affects predator-prey interactions (Power 1992). Predatory fish are usually size-selective, preferring moderate to large prey over small prey (Wellborn *et al.* 1996) but structural complexity generally reduces their impacts on macroinvertebrates (Diehl 1988, 1992, Warfe & Barmuta 2006). An assessment of differences in body sizes of ephemeropteran nymphs, coenagrionid naiads and chironomid larvae associated with the two plants tested the hypothesis that differences in macrophyte morphological complexity would result in differences in the impact of fish predation and so in differences in body size-class distributions of the insects. Since epiphytic macroinvertebrate assemblages can be affected by variation water physicochemical conditions (Cañedo-Argüelles & Rieradevall 2009), and so the effect of the physicochemical environment during the study period was also assessed.

3.2 Materials and Methods

This study was done over a period of three months, May to July in 2005. Samples of epiphytic invertebrates associated with *Lagarosiphon* and *Vallisneria* as well as water samples for assessing selected physicochemical variables were collected monthly from the sampling sites. Each site was also characterised on the basis of the main human activities and developments occurring with 500m of the shoreline, from which a human disturbance score was obtained. For sites 1 and 2, macroinvertebrate samples presented here are for the month of May only, due to spoilage of samples obtained in June and July. The methods and materials used in this study are described in section 2.3.1.

3.3 Results

3.3.1 Site characterisation and water physicochemical variation among sites

The results of site characterisation on the basis of notable human activities occurring within 500m of the shoreline at each site are presented in Appendix 2. None of the sites was categorized as being highly disturbed. The results of water physical and chemical variables measured at the sites are shown in Appendix 3. The variations in water physicochemical variables among sites are presented and discussed in detail by Phiri *et al.* (2007) (Appendix 4). The only variables that differed significantly among sites were pH and turbidity. The water at Sites 2, 3 and 6 had significantly greater average pH than that at Sites 4, 5, 7, 9 and 10, while pH at Site 3 was also significantly greater than at Site 8 (ANOVA, $F_{9, 17} = 4.03$, $p < 0.05$). Turbidity at Site 2 was significantly greater than that at Sites 4 and 5, while at Site 6 it was significantly greater than that at Sites 3, 7, 8, 9 and 10 (ANOVA, $F_{9, 17} = 2.55$, $p < 0.05$).

3.3.2 Spatial distribution of *Lagarosiphon* and *Vallisneria*

Vallisneria was present at all ten sites during the study period. Although *Lagarosiphon* tended to be the more dominant submerged plant at most sites, it was absent from site 4, which receives effluent from an adjacent crocodile breeding farm. The *Lagarosiphon* samples from site 7 and 9, as well as one *Vallisneria* sample from site 4, which were all obtained in May 2005 are omitted from the analysis as they were without invertebrates. Sites 7 and 9 were both within harbours, characterised by relatively high levels of boating activities as well as the maintenance and repay of boats (see Appendices 2 and 4).

3.3.3. Spatial aspects of invertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*

Table 3.1 shows the average taxa richness and abundance per gram dry mass of plant matter, invertebrate assemblage diversity associated with the two plant species and the dry mass of each plant collected from each site. The mean vegetation dry mass (ANOVA, $F_{14, 27} = 1.65$, $p = 0.13$), invertebrate taxa richness per gram of vegetation (ANOVA, $F_{14, 27} = 1.28$, $p = 0.28$) and invertebrate assemblage diversity (ANOVA, $F_{14, 27} = 198$, $p = 0.06$) did not differ significantly among sites for both plant species and between the two plants.

The average total invertebrate abundance on *Lagarosiphon* (ANOVA, $F_{6, 12} = 0.601$, $p = 0.72$) and *Vallisneria* (ANOVA, $F_{7, 15} = 2.261$, $p = 0.09$) did not significantly differ among sites. Significant differences in total invertebrate abundance were recorded between *Lagarosiphon* and *Vallisneria* (ANOVA, $F_{14, 27} = 3.93$, $p = 0.001$), with invertebrate numbers on *Lagarosiphon* from sites 3 and 7 significantly greater than abundances on *Vallisneria* from sites 8, 9 and 10 (Tukey Q tests, $p < 0.05$).

3.3.4 Effect of water physicochemical variables on macroinvertebrate assemblage structure

The variations in temperature, pH, turbidity and in concentrations of dissolved oxygen, ammonium, nitrates, phosphates and total phosphorus were not significantly correlated with number of taxa, total abundance and diversity of macroinvertebrate on *Lagarosiphon* (Spearman Rank correlation, $p > 0.05$). Water conductivity was significantly and negatively correlated with number of taxa on *Lagarosiphon* (Spearman r = -0.418, $p = 0.047$). Water turbidity (Spearman r = 0.524, $p = 0.007$) and total phosphorus concentration (Spearman r = 0.432, $p = 0.031$) were positively and significantly correlated with invertebrate abundance, while dissolved oxygen concentration (Spearman r = 0.403, p = 0.046) was significantly and positively correlated with invertebrate diversity on *Vallisneria*.

On both *Lagarosiphon* and *Vallisneria*, none of the three invertebrate assemblage structure indices were significantly correlated with the human disturbance score (Spearman, $p > 0.05$).

3.3.5 Comparative assessment of epiphytic invertebrates associated with *Lagarosiphon* and *Vallisneria*

The minimum and maximum numbers of macroinvertebrates collected from *Lagarosiphon* were 9.9 and 128.2 per g plant dry mass respectively, compared to 0.8 and 25.0 for *Vallisneria*. The overall mean macroinvertebrate abundance associated with *Lagarosiphon* (40.9 ± 7.3) was significantly greater than that on *Vallisneria* (7.8 ± 1.4) (Wilcoxon signed rank test, W = 228.0, $p < 0.001$) (Table 3.2). The number of taxa obtained from the two macrophytes was generally same (Wilcoxon signed rank test, W = 152.0, p = 0.687) (Table 3.2). The Shannon diversity index of the macroinvertebrate assemblage was not significantly different between the two plants species (Wilcoxon signed rank test, W = 170, p = 0.345).

Table 3.1. Mean values of the plant dry mass sampled for epiphytic invertebrates, and invertebrate taxa richness, total abundance and diversity (*H'*) on *Lagarosiphon* and *Vallisneria*. Richness and abundance are reported per gram dry mass of plant sampled. Numbers of samples (n) = 3, unless otherwise stated in brackets.

Site	Plant dry mass (g)		Richness		Abundance		Diversity (*H'*)	
	Lagarosiphon	*Vallisneria*	*Lagarosiphon*	*Vallisneria*	*Lagarosiphon*	*Vallisneria*	*Lagarosiphon*	*Vallisneria*
1	24.6 (n = 1)	13.3 (n = 1)	0.93 (n = 1)	0.75 (n = 1)	40.7 (n = 1)	2.8 (n = 1)	2.26 (n = 1)	1.87 (n = 1)
2	46.7 (n = 1)	19.2 (n = 1)	0.47 (n = 1)	0.88 (n = 1)	33.0 (n = 1)	4.7 (n = 1)	1.75 (n = 1)	2.20 (n = 1)
3	24.2 ± 10.7	22.2 ± 7.6	0.76 ± 0.19	0.80 ± 0.29	41.8 ± 25.4	8.6 ± 3.7	2.12 ± 0.35	2.07 ± 0.10
4	*Lagarosiphon* absent	40.2 ± 26.3 (n = 2)	*Lagarosiphon* absent	0.52 ± 0.28 (n = 2)	*Lagarosiphon* absent	18.0 ± 3.1	*Lagarosiphon* absent	1.81 ± 0.43
5	27.8 ± 7.4	19.0 ± 2.5	0.84 ± 0.22	1.00 ± 0.31	31.9 ± 11.5	7.2 ± 1.7	2.41 ± 0.07	2.46 ± 0.156
6	18.2 ± 2.7	18.0 ± 3.5	1.21 ± 0.36	1.06 ± 0.11	67.3 ± 32.2	17.0 ± 5.7	2.16 ± 0.16	2.03 ± 0.21
7	22.4 ± 7.4 (n = 2)	10.1 ± 2.4	0.72 ± 0.08 (n = 2)	1.18 ± 0.18	21.5 ± 0.4 (n = 2)	6.9 ± 3.1	1.33 ± 0.21 (n = 2)	1.73 ± 0.12
8	24.6 ± 3.2	13.0 ± 1.6	0.75 ± 0.19	0.84 ± 0.38	33.0 ± 19.0	6.7 ± 4.3	1.89 ± 0.12	1.27 ± 0.48
9	10.4 ± 1.5 (n = 2)	14.0 ± 2.6	1.42 ± 0.15 (n = 2)	0.87 ± 0.04	20.3 ± 3.3 (n = 2)	5.0 ± 2.9	1.91 ± 0.29 (n = 2)	1.94 ± 0.02
10	12.1 ± 1.7	10.9 ± 2.4	1.66 ± 0.38	0.83 ± 0.14	59.6 ± 26.3	2.4 ± 0.1	2.13 ± 0.23	1.94 ± 0.13

Table 3.2. The mean community indices of macroinvertebrates associated with *Lagarosiphon* and *Vallisneria.* The test static (W) of the Wilcoxon paired sample signed rank test and the *p* values are shown.

Index	*Lagarosiphon* (n=21)	*Vallisneria* (n=25)	Test statistic	*p* value
Mean total abundance (no. per g of plant)	40.9 ± 7.3	7.8 ± 1.4	228.0	<0.001
Richness (no. of taxa per g of plant)	0.99 ± 0.11	0.93 ± 0.07	152.0	0.687
Shannon Diversity index (*H'*)	2.03 ± 0.09	1.92 ± 0.09	170.0	0.345

Table 3.3 shows the abundances and frequency of occurrence of macroinvertebrates that were associated with *Lagarosiphon* and *Vallisneria*. A total of fifty-six macroinvertebrate taxa were obtained from the two macrophytes, and of these sixteen taxa were dominant on both plants. Forty-eight taxa were collected from *Lagarosiphon* compared to forty-five from *Vallisneria*. In order of decreasing abundance, the most abundant and frequently occurring taxa on *Lagarosiphon* were Chironominae, Naididae, *Caenis* sp., *Cloeon* sp., *Dugesia* sp., Orthocladiinae, *Bulinus depressus*, *Lymnaea columella*, *Physa acuta*, *Pseudagrion* sp., *Orthotrichia* sp., *Melanoides tuberculata*, Acari and Ostracoda (Table 3.3), which together made up 89.0% of the total number of organisms collected from *Lagarosiphon*. With respect to macroinvertebrate orders, Diptera, Gastropoda, Ephemeroptera and Odonata with percent relative abundance of 26.3%, 25.0%, 17.1% and 6.7% respectively, dominated the macroinvertebrate assemblage on *Lagarosiphon* (Table 3.3). Twelve taxa, *M. tuberculata*, *B. depressus*, Orthocladiinae, Chironominae, *Caenis* sp., *L. columella*, *Dugesia* sp., *Orthotrichia* sp., *Cloeon* sp., Naididae, Ostracoda and *P. acuta* made up 81.8% of the total macroinvertebrate abundance associated with *Vallisneria*. The gastropods, with a relative percent abundance of 44.7%, dominated the macroinvertebrate assemblage on *Vallisneria* followed by Diptera (20.8%), Ephemeroptera (9.1%) and Odonata (6.6%).

Table 3.3. Macroinvertebrates associated with *Lagarosiphon* and *Vallisneria* in the Lake Kariba (May to July 2005). n = number of samples, MA = mean abundance (no. per gram of plant dry mass) ± SE, %MRA = mean percent relative abundance, % Freq = percent frequency of occurrence, √ = present in low numbers and frequency, and − = absent.

			Lagarosiphon (n = 21)			*Vallisneria* (n = 25)		
Order	**Family**	**Taxa**	MA	%MRA	%Freq	MA	%MRA	%Freq
Rhynchobdellidae	Planariidae	*Dugesia* sp.	2.5 ± 1.4	4.6 ± 2.0	71.4	√	√	√
Oligochaeta[1]	Naididae	Naididae	4.1 ± 0.9	10.4 ± 1.9	90.5	0.3 ± 0.1	4.4 ± 1.5	68.0
Nematoda		Nematoda	√	√	√	–	–	–
Hirudinae	Glossiphonidae	*Alboglossiphonia* sp.	√	√	√	√	√	√
Gastropoda			8.3 ± 2.3	25.0 ± 4.8	95	3.4 ± 0.8	44.7 ± 5.5	100.0
	Hydrobiidae	*Lobogenes* sp.	√	√	√	√	√	√
	Lymnaedae	*Lymnaea columella*	2.1 ± 0.9	8.3 ± 3.8	76.2	0.7 ± 0.2	12.6 ± 3.4	84.0
	Physidae	*Physa acuta*	1.7 ± 0.6	4.6 ± 1.5	71.4	0.2 ± 0.1	5.0 ± 1.6	52.0
	Planorbidae	*Bulinus depressus*	2.3 ± 0.8	6.4 ± 2.1	90.5	0.9 ± 0.3	11.6 ± 2.8	76.0
		Bulinus forskalii	√	√	√	√	√	√
		Biomphalaria pfeiferri	√	√	√	√	√	√
	Thiaridae	*Cleopatra nsedwensis*	√	√	√	√	√	√
		Melanoides tuberculata	1.1 ± 0.7	1.9 ± 1.0	47.6	1.1 ± 0.5	8.9 ± 3.7	48.0
	Viviparidae	*Bellamya capillata*	√	√	√	√	√	√
	Anyclidae	*Ferrisia* sp.	√	√	√	√	√	√
	Sphaeridae	*Sphaerium* sp.	√	√	√	√	√	√
Hydracarina		Acari	1.0 ± 0.5	1.5 ± 0.5	71.4	√	√	√
Cladocera	Daphniidae	*Daphnia* sp.	–	–	–	√	√	√
Cyclopoida	Cyclopoida	Cyclopoida	√	√	√	√	√	√
Conchostraca	Cyclestheriidae	*Cyclestheria hislopi*	√	√	√	√	√	√

[1] Largely Naididae

Table 3.3. Continued

			Lagarosiphon (n = 21)			*Vallisneria* (n = 25)		
Order	**Family**	**Taxa**	MA	%MRA	%Freq	MA	%MRA	%Freq
Ostracoda		Ostracoda	1.0 ± 0.5	1.8 ± 0.7	61.9	0.3 ± 0.2	2.2 ± 1.3	32.0
Collembola	Isotomidae	Isotomidae	√	√	√	√	√	√
	Poduridae	Poduridae	√	√	√	–	–	–
Ephemeroptera			7.3 ± 1.9	17.1 ± 3.4	100.0	1.1 ± 0.5	9.1 ± 2.6	68.0
	Polymitarcyidae	*Povilla* sp	–	–	–	√	√	√
	Caenidae	*Caenis* sp	3.9 ± 1.2	9.6 ± 3.2	76.2	0.8 ± 0.5	5.5 ± 2.3	36.0
	Baetidae	*Cloeon* sp	3.3 ± 1.0	7.4 ± 1.7	95.2	0.3 ± 0.1	3.5 ± 1.1	52.0
Odonata			2.5 ± 1.1	6.7 ± 1.8	100.0	0.3 ± 0.1	6.6 ± 1.6	80.0
	Coenagrionidae	*Pseudagrion* sp	1.5 ± 0.8	3.4 ± 0.9	100.0	√	√	√
		Enallagma sp	√	√	√	√	√	√
		Ischnura sp	0.7 ± 0.3	2.2 ± 0.7	81.0	√	√	√
	Gomphidae	*Ictinogomphus* sp	√	√	√	√	√	√
		Notogomphus sp	√	√	√	–	–	–
	Cordulidae	*Phyllomacromia* sp	√	√	√	–	–	–
		Hemicordulia sp	√	√	√	√	√	√
	Lestidae	*Lestes* sp	√	√	√	–	–	–
	Libellulidae	*Pantala* sp	–	–	–	√	√	√
		Bradinopyga sp	√	√	√	√	√	√
		Trithemis sp	√	√	√	√	√	√
		Zyxomma sp	–	–	–	√	√	√

Table 3.3. Continued

			Lagarosiphon (n = 21)			*Vallisneria* (n = 25)		
Order	**Family**	Taxa	MA	%MRA	%Freq	MA	%MRA	%Freq
Hemiptera	Belostomatidae	*Appasus* sp	–	–	–	√	√	√
	Corixidae	*Micronecta* sp	√	√	√	√	√	√
	Pleidae	*Plea* sp	√	√	√	–	–	–
Coleoptera	Dysticidae	*Dysticus* sp	√	√	√	–	–	–
	Curculionidae	*Neochetina* sp	√	√	√	–	–	–
Trichoptera			1.9 ± 0.6	4.7 ± 1.3	90.5	0.4 ± 0.2	4.9 ± 1.5	68.0
	Hydroptilidae	*Orthotrichia* sp	1.1 ± 0.4	2.8 ± 1.0	71.4	0.3 ± 0.1	3.8 ± 1.4	40.0
	Ecnomidae	*Ecnomus* sp	0.8 ± 0.3	1.8 ± 0.5	81.0	√	√	√
	Leptoceridae	*Leptocerina* sp	–	–	–	√	√	√
	Leptoceridae	*Athripsoides* sp	–	–	–	√	√	√
	Philopotamidae	Philopotamidae	√	√	√	–	–	–
Lepidoptera	Crambidae	*Nymphula* sp	√	√	√	√	√	√
Diptera			11.4 ± 3.6	26.3 ± 4.6	100	1.9 ± 0.5	20.8 ± 3.6	92.0
	Ceratopogonidae	*Bezzia* sp	–	–	–	√	√	√
	Chaoboridae	*Chaoborus* sp	√	√	√	–	–	–
	Chironomidae	Chironominae	8.2 ± 2.6	18.9 ± 3.3	100.0	0.8 ± 0.2	11.1 ± 2.1	88.0
		Tanypodinae	√	√	√	√	√	√
		Orthocladiinae	2.4 ± 0.7	5.9 ± 1.1	81.0	0.9 ± 0.4	7.1 ± 2.5	64.0
	Culicidae	*Anopheles* sp	√	√	√	–	–	–
		Culex sp	√	√	√	–	–	–
	Sciomyzidae	Sciomyzidae	√	√	√	√	√	√

Thus, the macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria* largely comprised the same taxa. Figure 3.1 shows that the abundances of the most dominant and common taxa were generally greater on *Lagarosiphon* than on *Vallisneria* at all sampling sites. The minimum and maximum range in abundance for each of these taxa recorded in association with *Lagarosiphon* were; *Dugesia* sp (0.0 – 28.9 per g dry mass of plant material), Oligochaeta (0.0 – 15.0), *L. columella* (0.0 – 15.2), *P. acuta* (0.0 – 9.4), *B. depressus* (0.0 – 15.4), *M. tuberculata* (0.0 – 14.5), *Caenis* sp (0.0 – 15.9), *Cloeon* sp (0.0 – 14.5), Coenagrionidae (0.04 – 22.9), Trichoptera (0.0 – 12.7), Chironominae (0.3 – 54.6) and Orthocladiinae (0.0 – 14.0). Comparatively, the minimum and maximum range in abundance of the same taxa on *Vallisneria* were; *Dugesia* sp (0.0 – 1.2), Oligochaeta (0.0 – 0.8), *L. columella* (0.0 – 2.3), *P. acuta* (0.0 – 0.7), *B. depressus* (0.0 – 7.6), *M. tuberculata* (0.0 – 11.1), *Caenis* sp (0.0 – 11.9), *Cloeon* sp (0.0 – 2.6), Coenagrionidae (0.0 – 1.4), Trichoptera (0.0 – 3.5), Chironominae (0.0 – 3.2) and Orthocladiinae (0.0 – 10.0). On *Lagarosiphon* the highest values in abundances of collectors, filterers, grazers and predators were; 108.3, 3.1, 47.1 and 43.6 per g of plant dry mass, whilst on *Vallisneria* there were 17.1, 1.1, 11.8 and 3.9 respectively.

Table 3.4 shows the overall mean abundances of the common taxa and the functional feeding groups associated with the two plant species. The mean abundances of *Dugesia* sp., Naididae, *P. acuta*, *Caenis* sp., *Cloeon* sp., Coenagrionidae (*Ischnura* sp., *Enallagma* sp. and *Pseudagrion* sp.), Trichoptera (*Ecnomus* sp., *Orthotrichia* sp., *Athripsoides* sp., *Leptocerina* sp., and Philopotamidae), Chironominae and Orthocladiinae were significantly greater on *Lagarosiphon* than on *Vallisneria* (Wilcoxon signed rank tests, $p < 0.05$) (Table 3.4). The mean abundances of *L. columella*, *B. depressus*, and *M. tuberculata* were not significant between the two plant species (Wilcoxon signed rank tests, $p > 0.05$) (Table 3.4).

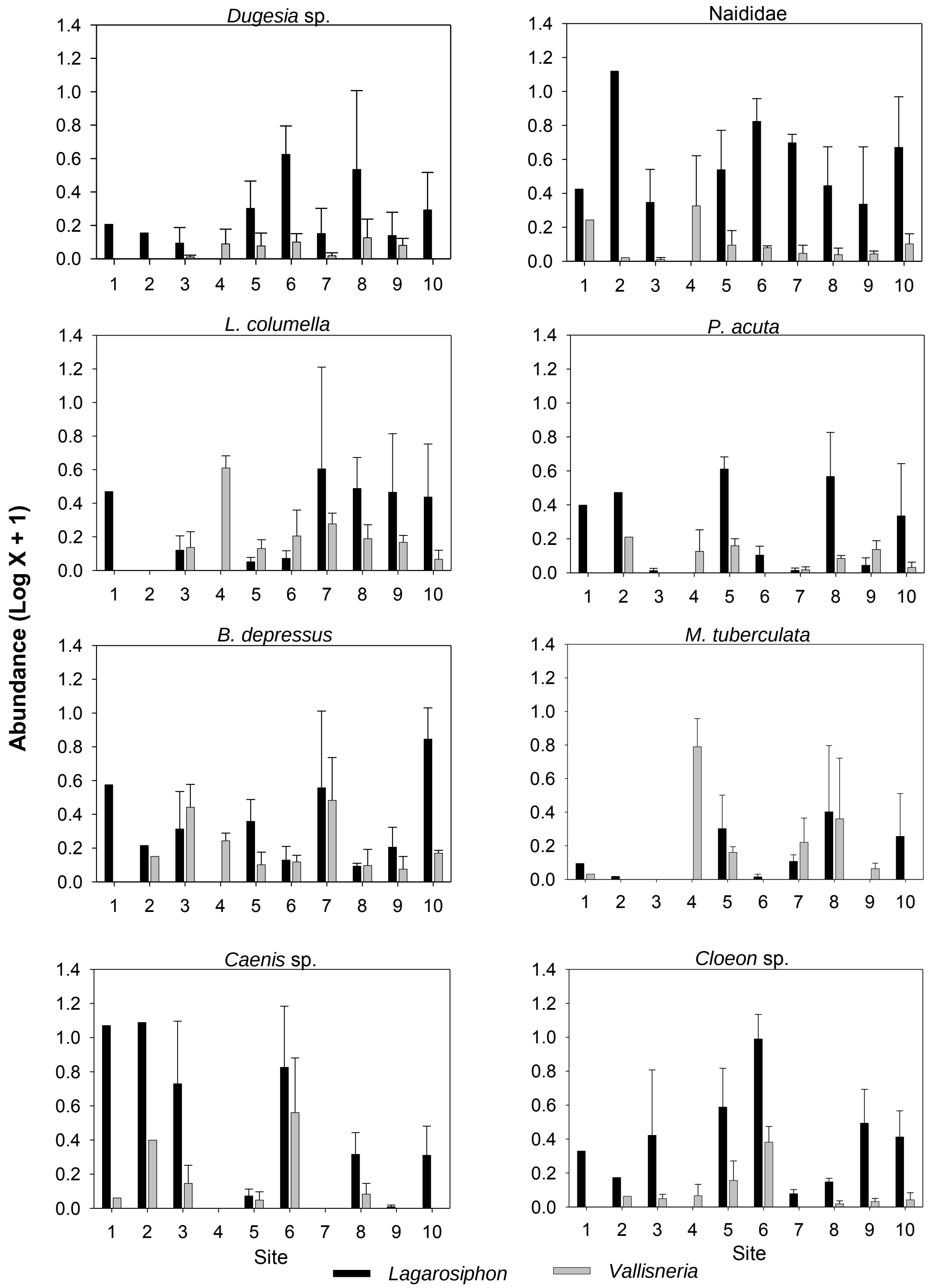

Figure 3.1. The mean abundances (no. per gram of plant dry mass) of the most abundant and frequently occurring macroinvertebrate taxa associated with *Lagarosiphon* **and** *Vallisneria*.

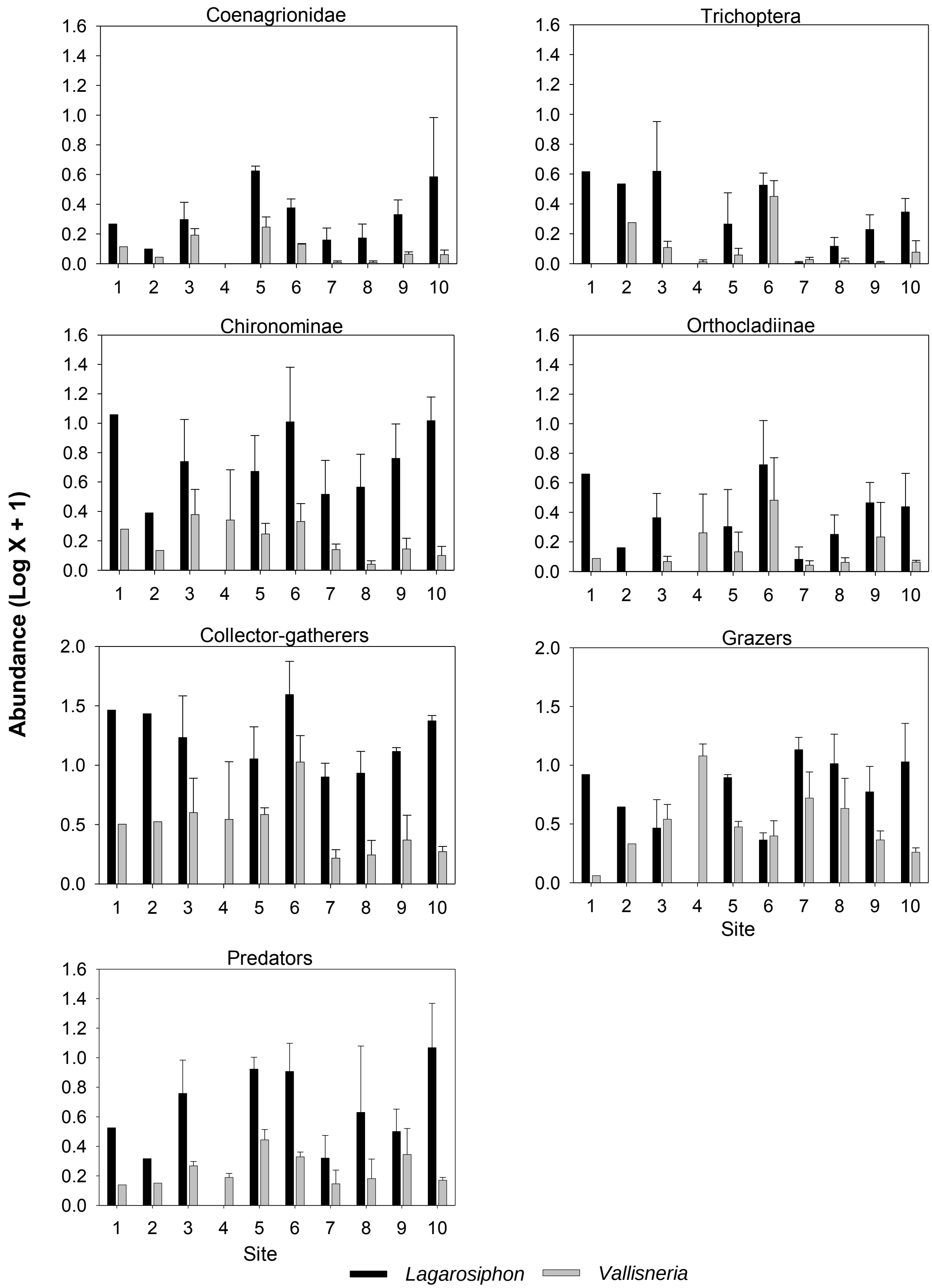

Figure 3.1. Continued.

The dipteran subfamily Chironominae dominated the epiphytic macroinvertebrate community on *Lagarosiphon*, with a mean abundance (8.2 ± 2.6), which was significantly greater than of most of the other taxa (Wilcoxon signed rank tests, $p < 0.05$), except for Naididae with which there was no significant difference (Wilcoxon signed rank test, $p > 0.05$).

On *Vallisneria*, the mean abundance of Chironominae was significantly greater than that of *Dugesia*, Naididae, P*. acuta*, *M. tubercuta*, *Cloeon*, Coenagrionidae and Trichoptera (Wilcoxon signed rank test, $p < 0.05$), but did not differ significantly from *L. columella*, *B. depressus* and *Caenis* (Wilcoxon signed rank test, $p > 0.05$).

The main macroinvertebrate functional feeding groups associated with the two macrophyte species were collector-gatherers, grazers and predators, with filterers occurring in low numbers on both plants (Table 3.4). Collector-gatherers, grazers and predators were significantly more abundant on *Lagarosiphon* than on *Vallisneria* (Wilcoxon signed rank tests, $p < 0.05$), whilst the abundance of collector-filterers did not differ between the two plant species (Wilcoxon signed rank test, $p > 0.05$). Collector-gatherers with an average abundance of 23.1 ± 5.4, made up nearly 60% of the total number of organisms associated with *Lagarosiphon*, and their abundance was significantly greater than those of the other functional feeding groups (Wilcoxon signed rank tests, $p < 0.05$). There was no significant difference in the abundances of grazers and predators on *Lagarosiphon* (Wilcoxon signed rank test, $p > 0.05$). Collector-filterers were significantly less abundant than the other three functional feeding groups on both *Lagarosiphon* and *Vallisneria* (Wilcoxon signed rank tests, $P < 0.05$). The mean abundances of collector gatherers and grazers on *Vallisneria* were not significantly different (Wilcoxon signed rank test, $p > 0.05$), but both were significantly greater than predators (Wilcoxon signed rank test, $p < 0.05$).

Analysis of the epiphytic macroinvertebrate assemblages of the two plant species using non- metric multidimensional scaling (MDS) showed a clear separation of macroinvertebrate communities (Figure 3.2). ANOSIM showed that there were significant differences in macroinvertebrate community structure associated with the

Lagarosiphon and *Vallisneria* (Grobal R = 0.356, P < 0.001), with high average dissimilarity of 72.03%. Fourteen taxa were identified by SIMPER as significantly contributing to differences in macroinvertebrate community structure of the two plant species (Table 3.5). All fourteen taxa occurred on both plant species and SIMPER also showed that with the exception of *M. tuberculata,* which was slightly more abundant on *Vallisneria*, most taxa were generally much more abundant on *Lagarosiphon* (Table 3.5).

Table 3.4. Results of comparison of differences using the Wilcoxon signed rank test in mean abundances (no. per gram plant dry mass) of major taxa and functional feeding groups associated with *Lagarosiphon* **and** *Vallisneria* **.** *p* **values that were significant are in bold.**

Taxa	*Lagarosiphon* (n = 21)	*Vallisneria* (n = 25)	*p*-value
Dugesia	2.5 ± 1.4	0.2 ± 0.1	**0.001**
Naididae	4.1 ± 0.9	0.2 ± 0.1	<**0.001**
L. columella	2.1 ± 0.9	0.5 ± 0.1	0.312
P. acuta	1.7 ± 0.6	0.2 ± 0.1	**0.002**
B. depressus	2.3 ± 0.8	1.0 ± 0.4	0.128
M. tuberculata	1.2 ± 0.7	0.7 ± 0.5	0.569
Caenis	3.9 ± 1.2	0.9 ± 0.6	**0.004**
Cloeon	3.3 ± 1.0	0.4 ± 0.1	<**0.001**
Coenagrionidae	2.3 ± 1.1	0.3 ± 0.1	<**0.001**
Trichoptera	1.9 ± 0.6	0.4 ± 0.2	**0.003**
Chironominae	8.2 ± 2.6	0.8 ± 0.2	<**0.001**
Orthocladiinae	2.4 ± 0.7	0.9 ± 0.5	**0.015**
FFG			
Collector-gatherers	23.1 ± 5.4	3.6 ± 1.1	<**0.001**
Filterers	0.3 ± 0.2	0.1 ± 0.1	0.129
Grazers	8.3 ± 2.3	2.7 ± 0.7	<**0.001**
Predators	8.0 ± 2.4	1.0 ± 0.2	<**0.001**

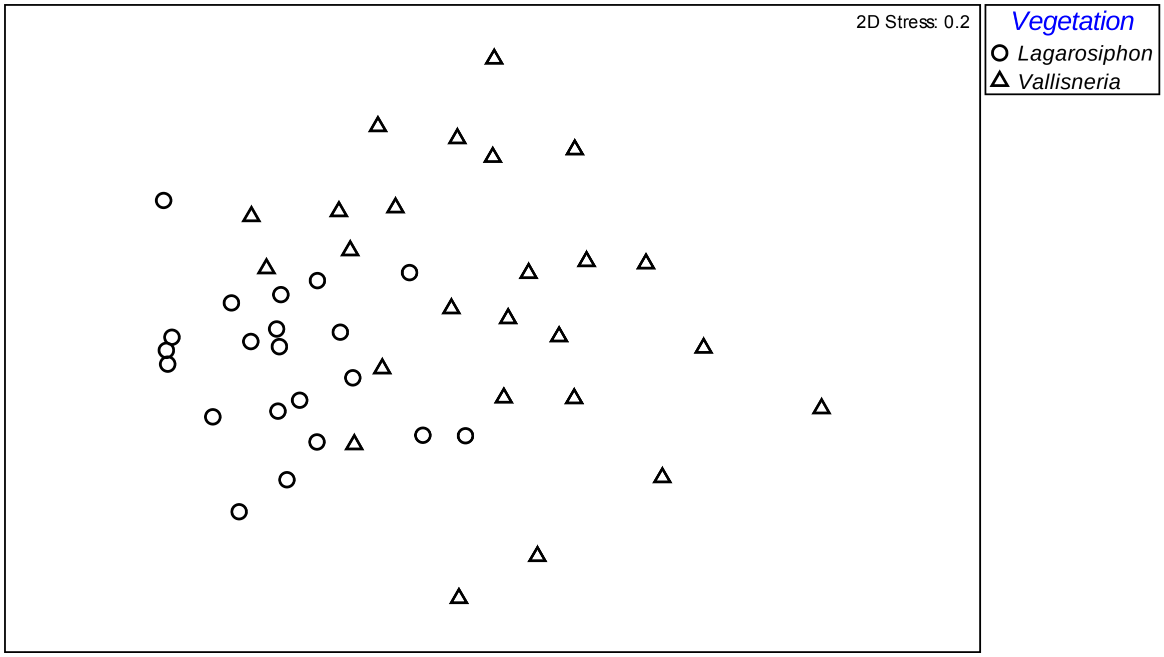

Figure 3.2. The nMDS plot of epiphytic macroinvertebrate communities associated with *Lagarosiphon* and *Vallisneria* in the Sanyati Basin.

Table 3.5. Taxa identified by SIMPER as making significant contributions to the dissimilarity in macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*.

Taxa	*Lagarosiphon* (n = 21)	*Vallisneria* (n = 25)			
	Average Abundance	Average Abundance	Average Dissimilarity	Contribution (%)	Cumulative (%)
Chironominae	0.76	0.21	8.53	11.85	11.85
Oligochaeta	0.58	0.09	7.51	10.43	22.28
Caenis sp	0.43	0.12	6.06	8.41	30.69
Cloeon sp	0.44	0.09	5.43	7.54	38.23
Orthocladiinae	0.39	0.15	5.33	7.39	45.62
L. columella	0.29	0.19	5.01	6.95	52.57
B. depressus	0.36	0.20	4.81	6.68	59.25
P. acuta	0.28	0.07	4.02	5.58	64.83
Dugesia sp	0.31	0.06	3.83	5.32	70.15
M. tuberculata	0.15	0.16	3.43	4.77	74.91
Orthotrichia sp	0.22	0.08	3.29	4.57	79.48
Pseudagrion sp	0.27	0.06	3.10	4.3	83.79
Ostracoda	0.18	0.07	2.55	3.54	87.32
Ischnura sp	0.17	0.03	2.52	3.5	90.83
Average Dissimilarity	72.03				

The size class distributions of *Cloeon*, *Caenis*, Coenagrionidae (*Pseudagrion*, *Ischnura* and *Enallagma*) and Chironomids (Chironominae and Orthocladiinae) are shown in Figure 3.3. The size class spectrum of both *Cloeon* nymphs and coenagrionid naiads differed significantly between the two plants (Kolmogorov-Smirnov two sample test, $p < 0.05$). A significantly greater proportion of bigger size classes of *Cloeon* were associated with *Lagarosiphon* compared with *Vallisneria* (Kolmogorov-Smirnov test, D = 0.364, $p = 0.025$) while for coenagrionid naiads, significantly greater proportion of larger size classes occurred on *Vallisneria* than on *Lagarosiphon* (Kolomogorov-Smirnov test, D = 0.263, $p = 0.041$). No significant differences were observed in the size class distributions of *Caenis* nymphs (Kolmogorov-Smirnov test, D = 0.267, $p = 0.386$) and Chironomid larvae (Kolmogorov-Smirnov, D = 0.200, $p = 0.938$) between *Lagarosiphon* and *Vallisneria*.

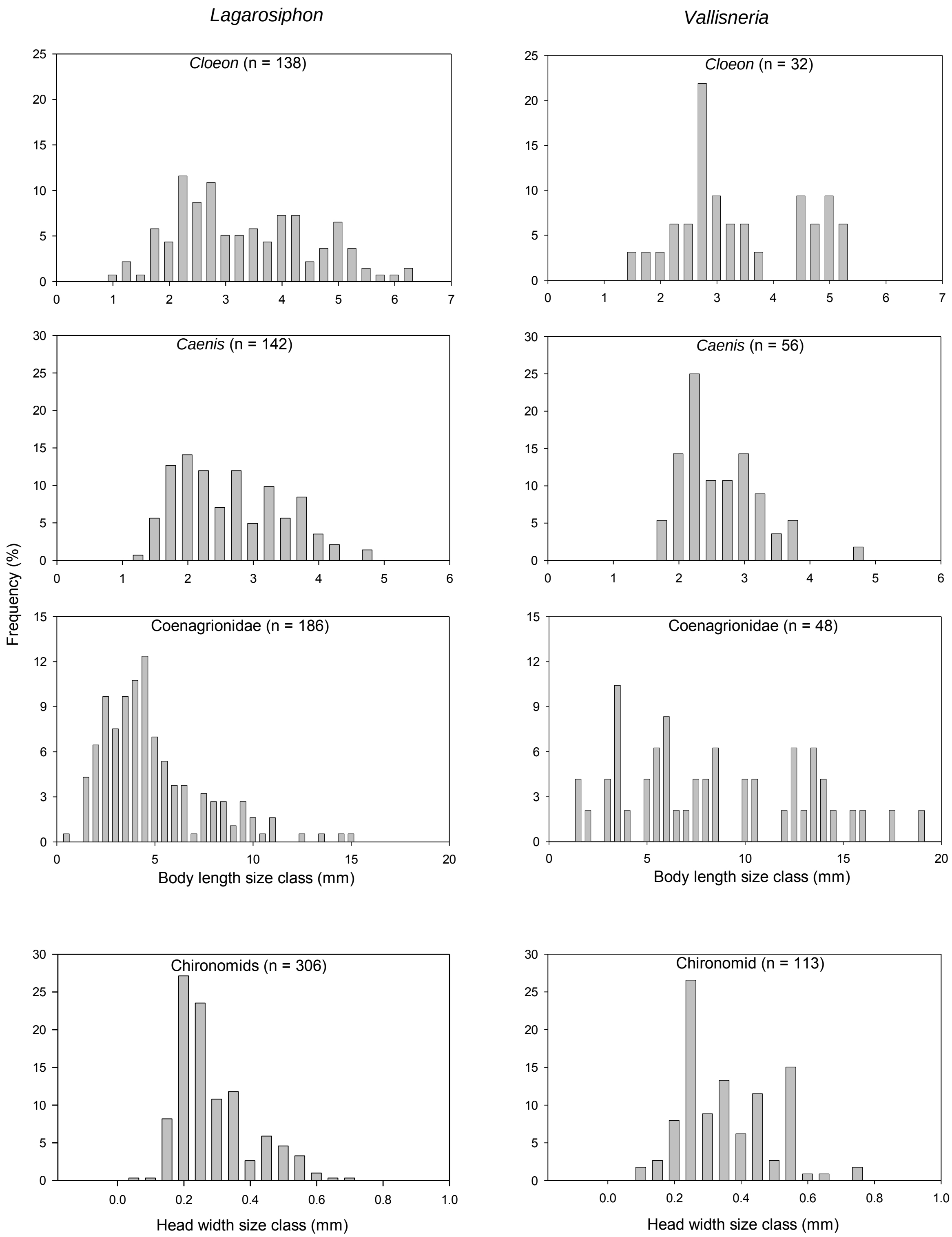

Figure 3.3. Body length size distribution for *Cloeon, Caenis* and Coenagrionidae, **and head-width size distribution for chironomids associated with** *Lagarosiphon* and *Vallisneria* **in Lake Kariba.**

3.4 Discussion

3.4.1 Physicochemical environment and its effect on epiphytic invertebrates

Qualitative classification of sampling sites based on shoreline activities classified most of the sites as being moderately affected by human activities. The number of invertebrate taxa per gram, total abundance and assemblage diversity on both *Lagarosiphon* and *Vallisneria* were not significantly affected by variation in human activities along the shoreline. Interestingly though, samples of *Lagarosiphon* obtained from sites 7 and 9, and *Vallisneria* from site 4 in May 2005 had no macroinvertebrates. Although the cause of these observations could not be definitely ascertained, it is plausible to suggest that human activities at the three sites were to some extent responsible. Effluent disposal from crocodile farming was a major characteristic of site 4, while high levels of boating and boat maintenance activities characterised sites 7 and 9. Also notable was the absence of *Lagarosiphon* at site 4 during the study period. Boating activities have been shown to have negative effects on macrophytes, invertebrates and fish (Wolter & Arlinghaus 2003, Eriksson *et al.* 2004, Gutreuter *et al.* 2006, Kucera-Hirzinger *et al*. 2009). Aquaculture effluents may contain a variety of constituents, such as therapeutants, disinfectants, water treatment compounds, algaecides, herbicides and feed additives, which can cause negative impacts when released into the environment (Piedrahita 2003). This study suggests that impacts of aquaculture effluent disposal and boating activities on plant and invertebrate assemblages in Lake Kariba requires further investigation.

During the study there were no significant correlations between most of the water physicochemical variables that were measured and the three indices of macroinvertebrate community structure (richness, abundance and diversity) on both *Lagarosiphon* and *Vallisneria*. The number of taxa on *Lagarosiphon* generally decreased with increase in conductivity. On *Vallisneria*, the increase in turbidity and total phosphorus were associated with significant increases in total invertebrate abundance, and oxygen concentration was positively correlated with invertebrate assemblage diversity. Variation in conductivity has been shown to affect macroinvertebrate assemblages (Black *et al*. 2004). In streams of the Puget Sound Basin (USA) Black *et al.* (2004) showed that macroinvertebrate taxa composition was strongly correlated with conductivity. The range in water conductivity of the streams in which Black *et al.* (2004) did their study was from 9.96 to 2 510 μS/cm. In the current study the minimum and maximum values in conductivity were 94 and 104.5 μS/cm respectively. Thus in this study the differences in conductivity among sites and dates were small and it is therefore unlikely that conductivity had a great impact on invertebrate assemblages on both plants. Increase in turbidity and nutrients in water may occur when sediments and other materials enter the water column (Baxter 1997, Rosenberg *et al.* 2000). Fish predation on invertebrates generally occurs through visual detection and increase in water turbidity may adversely affect their detection of prey (Horppila & Liljendahl-Nurminen 2005, Liljendahl-Nurminen *et al*. 2008). According to Liljendahl-Nurminen *et al*. (2008) water turbidity can strongly regulate the abundance and species composition of invertebrate assemblages. Therefore, the observed positive relationship between turbidity and invertebrate abundance on *Vallisneria* was possibly a result of reduction in the success rate fish of predation on invertebrates as turbidity increased.

Generally, there is need for more studies on the effect of water physicochemical in structuring macroinvertebrate communities in Lake Kariba, especially with the view of developing monitoring strategies of human activities in shallow marginal waters of Lake Kariba. In a related study Phiri *et al.* (2007) found that periphytic diatoms associated with V*allisneria* are potentially useful in assessing ecological conditions or the impact of human activities within the shallow marginal waters of Lake Kariba. Although in this study an attempt was made to relate invertebrate assemblages associated with *Lagarosiphon* and *Vallisneria* to human activities and water physicochemical variables, the main focus of the study was on differences in invertebrate assemblages associated with the two plant species.

3.4.2 Comparative assessment of invertebrate assemblages on *Lagarosiphon* and *Vallisneria*

The macroinvertebrate communities on both *Lagarosiphon* and *Vallisneria* were dominated by fourteen taxa: *Dugesia* sp, Oligochaeta, *L. columella, P. acuta*, *B. depressus*, *M. tuberculata*, Ostracoda, *Caenis* sp, *Cloeon* sp, *Pseudagrion*, *Ischnura*, *Orthotrichia*, Chironominae and Orthocladiinae. Although the two plant species were characterised by similar epiphytic macroinvertebrate assemblages, most taxa occurred in much greater abundance on *Lagarosiphon*. The differences in macroinvertebrate community can be attributed to differences in the physical morphology of the two plants.

The small but numerous leaves on the stems of *Lagarosiphon* create a more complex habitat, which harbours larger quantities of particulate organic matter as well as providing more attachment surfaces for invertebrates than the long strips of leaves of *Vallisneria*. The surfaces of macrophytes with complex morphologies have been shown not only to trap greater amounts of fine and coarse particulate organic matter (Rooke 1984, 1986a), but also have greater amounts of periphyton (Warfe & Barmuta 2006), which are an important food source for many epiphytic invertebrates. Complex morphology also provides better refuge for invertebrates from fish predation (Irvine *et al.* 1990, Cheruvelil *et al.* 2002). Thus the greater morphological complexity of *Lagarosiphon* possibly increased food availability and protection from predation for macroinvertebrates and so resulted in much greater abundances of macroinvertebrates, especially collector-gatherers. A number of studies have found similar results when comparing differences in epiphytic macroinvertebrate abundances between macrophytes of differing morphological complexity (e.g., Jackson 1997, Cattaneo *et al.* 1998, Bogut *et al.* 2007). Cheruvelil *et al.* (2000) also found that for macrophyte species with similar morphological structure there were no differences in the abundance of macroinvertebrates.

On both plants the Chironomidae, was largely represented by the subfamilies of Chironominae and Orthacladiinae, with small numbers of Tanypodinae. The abundances of all three subfamilies were much greater on *Lagarosiphon* than on *Vallisneria*. The Naididae also made up a significant portion of the macroinvertebrate community on *Lagarosiphon*. Chironomids inhabit all freshwater bodies, and are among the most successful aquatic macroinvertebrate taxa (Mackie 2001). They often form a major proportion of epiphytic macroinvertebrate communities (Learner *et al*. 1989, Dukowska *et al.* 2009). The dominance of Chironomidae in epiphytic macroinvertebrate assemblages of different aquatic plants has been observed in a number of studies (e.g., Tessier *et al.* 2004, Albertoni *et al.* 2007, Bogut *et al.* 2007). This has been attributed to their wide range of feeding behaviour and food preference (Lindegaard, in Nilsson 1997). Oligochaetes also tend to be among the most dominant macroinvertebrates associated with vegetation in freshwater environments (Botts & Cowell 1993).

Freshwater snails are a common component of the invertebrate fauna associated with submersed macrophytes (Brönmark 1989a, Li *et al.* 2009a, b). The snails generally feed on the periphytic algae/bacteria/detritus complex and decaying macrophyte tissue (Brönmark 1990). Eleven gastropod taxa occurred on both *Lagarosiphon* and *Vallisneria*, and four of these, *L. columella, P. acuta*, *B. depressus*, and *M. tuberculata* made up a significant proportion of macroinvertebrate community on both macrophyte species. On *Vallisneria*, *L. columella* (12.6%) and *B. depressus* (11.6%) were the most abundant of all the taxa. Gastropods were the second most abundant order after Diptera on *Lagarosipon* and were the most abundant order on *Vallisneria*. Thus food was generally available for snails on both plant species, but greater food concentration and refuge from fish predation probably resulted in overall greater snail numbers on *Lagarosiphon* compared to *Vallisneria*. A much increased proportion of snails on *Vallisneria* (44.7%) compared to *Lagarosiphon* (25%) suggests that the level of fish predation on snails on *Vallisneria* was less than predation on other macroinvertebrate taxa. In Lake Kariba there is only one fish species, the cichlid, *Sargochromis codringtonii*, that is known to largely feed on snails, and in a recent lake-wide survey, Zengeya & Marshall (2008) found that it contributed only 1.4% to the total number of fish collected from shallow bays.

Ephemeropteran nymphs colonize all types of freshwaters habitats but are more diversified in running waters than in lakes (Barber-James *et al.* 2008). They play an important role in almost all freshwater ecosystems (Beketov 2004) and are an important part of the aquatic food chain, consuming primary producers such as algae and plants, and as a food source for invertebrate and vertebrate predators (Brittain & Sartori 2003). Ephemeropteran nymphs contributed much greater numbers (17%) to macroinvertebrate fauna on *Lagarosiphon* than on *Vallisneria* (9%). *Caenis* and *Cloeon* were the two most common and abundant mayfly taxa associated with both plants. Two specimens of the third taxon *Povilla,* a burrower, were collected from two sites in association with *Vallisneria*. Although on both plants the abundance of *Caenis* was not significantly different from that of *Cloeon*, the latter was much more frequent and more widely distributed. In an earlier study, Bowmaker (1973) recorded three ephemeropteran taxa on *Lagarosiphon*, which were, *Euthraulus* sp, *Cloeon* sp and *Povilla adusta*, which made up 0.1%, 3.4% and 2.1% respectively, of the macroinvertebrate fauna, and also found that *Povilla* made up 63% of the fauna on inundated trees. *Euthraulus* was recorded as being generally present, while *Cloeon* and *Povilla* were numerous and commonly found on *Lagarosiphon*. Both this and Bowmaker's (1973) study show the widespread and common occurrence of *Cloeon* on *Lagarosiphon*, with the present study showing that it occurred less frequently and in much reduced numbers on *Vallisneria*. The current study also shows that *Euthraulus*, which tends to prefer stony-bottomed and slow-flowing waters (Barber-James & Lugo-Ortiz 2003) did not occur on both *Lagarosiphon* and *Vallisneria*, while *Povilla* infrequently occurred on *Vallisneria* and was not collected from *Lagarosiphon*. The study suggests possible reduction in occurrence or disappearance of *Euthraulus* and *Povilla* from the lake since the early studies in the late 1960s and early 1970s, although other substrates may need to be sampled to verify the findings. It is notable that none of the earlier work on macroinvertebrate fauna of Lake Kariba recorded the presence of *Caenis*, although according to Barber-James & Lugo-Ortiz (2003), the Caenidae family is found worldwide, with *Caenis* being the most common genius in the Afrotropics. Also of interest is the fact that in the current study ephemeropteran nymphs on average comprised 17%, while in Bowmaker's (1973) study they made up 5.5% of the macroinvertebrate fauna on *Lagarosiphon*. The low proportional contribution by *Cloeon* to the macroinvertebrate fauna associated with *Lagarosiphon* in the late 1960s and early 1970s may have been due to the low frequency of occurrence of submerged aquatic vegetation or the negative effects of high coverage of the water surface by the floating macrophyte *Salvinia molesta*.

Trichopterans are also important components of freshwater systems, contributing to the transfer of energy and nutrients through all trophic levels (Wiggins 1996). In this study, five caddisfly taxa were recorded but only two, *Orthotrichia* and *Ecnomus,* occurred in comparatively high numbers on the two macrophytes, and *Orthotrichia* tended to be more abundant than *Ecnomus* on both plants. Generally, both *Orthotrichia* and *Ecnomus* occurred in significantly greater numbers on *Lagarosiphon* than on *Vallisneria*. The work by Bowmaker (1973) recorded only one trichopteran species, *Ecnomus thomasseti* on submerged vegetation. The relative percent contribution of caddisfly nymphs to macroinvertebrate fauna on *Lagarosiphon* and *Vallisneria*, of 4.7% and 4.9% respectively, were generally greater than those reported by Bowmaker (1973) of less than 1% on *Ceratophyllum* and *Lagarosiphon*, and only 1.1% on *Potamogeton*. This study suggests that abundances and number of taxa of trichoptera in Lake Kariba have possibly increased since the early 1970s.

All odonates are dependent upon aquatic habitats for larval development (Rouquette & Thompson 2005). The most abundant odonate nymphs associated with *Lagarosiphon* and *Vallisneria* were the Coenagrionidae. Coenagrionidae are common in the littoral zones of lakes and are primarily associated with submerged vegetation (Miller *et al.* 1989, Bergey *et al.* 1992). They are generalist predators, feeding on the most common species of suitable size and their diet includes insects, oligochaetes, small crustaceans and molluscs (Hilsenhoff 1991). They consequently may play an important role at the top levels of invertebrate food webs (Hilsenhoff 1991). Anisopteran nymphs can be found in virtually every freshwater system (Misof 2002) and according Corbet (1999) they are generally the top insect predators and usually occur in high abundance. Although on both *Lagarosiphon* and *Vallisneria*, more anisopteran families (4) and genera (9) were recorded, compared to one zygopteran family (Coenagrionidae) (Table 3.3), the anisopteran nymphs were present in very lower numbers on both plant species. Three coenagrionid genera, *Pseudagrion*, *Enallagma* and *Ischnura,* were the most common and abundant large insect predators on both plants. The three damsel fly genera were much more abundant on *Lagarosiphon* than on *Vallisneria*. Miller *et al.* (1989) and Lombardo (1995) also found greater abundances of damselflies on architecturally complex macrophytes than on simple ones. The relative percent contribution of odonata nymphs to epiphytic macroinvertebrate fauna on *Lagarosiphon* (6.7%) and *Vallisneria* (6.6%), where generally similar to those recorded by Bowmaker (1973) on *Lagarosiphon* (6.2%), *Ceratophyllum* (7.1%) and *Potamogeton* (4.2%).

There were also differences in macroinvertebrate assemblages associated with the two submerged macrophytes with respect to functional feeding groups. Collector-gatherers dominated the functional macroinvertebrate assemblages of both macrophyte species, but with a much greater proportion on *Lagarosiphon*. This can be attributed to the greater morphological complexity of *Lagarosiphon* compared to *Vallisneria*, which provides more protection from predators as well as enhancing the accumulation of particulate matter on the plant surfaces and so greater concentrations of food for collector-gatherers.

The abundance of grazers, largely dominated by gastropods, was comparatively greater on *Lagarosiphon* than on *Vallisneria*, but the relative abundances of *L. columella*, *B. depressus* and *M. tuberculata* compared to other taxa were much greater on *Vallisneria*, resulting in the Gastropoda being the most dominant macroinvertebrate order on *Vallisneria*. Thus unlike *Lagarosiphon*, on which collector-gatherers were the most dominant functional feeding group, collector-gatherers and grazers, were equally dominant on *Vallisneria*. Snails have been shown to directly feed on living aquatic macrophytes (Sheldon 1987, Elger & Lemoine 2005, Li *et al.* 2009a, b), and on periphyton on the surface of plants (Brönmark 1985, 1989a, Li *et al.* 2009b) as well as use the plant surface to deposit eggs (Rooke 1984, Lodge 1985, Pinowska 2002). Periphyton is the dominant food base of littoral gastropods (Rooke 1984, 1986a, b) and grazing by snails can modify periphyton biomass, productivity and species composition (Brönmark 1985, 1989a, b). Differences in periphyton density among plants of varying architecture have been reported for several macrophyte taxa (Cattaneo & Kalff 1980, Allen & Ocevski 1981). The simpler ribbon like leaf morphology of *Vallisneria* may reduce self-shading, thus enabling light to reach greater proportions of the plant surface and so facilitating increased periphyton abundance. The simpler structure may also enable easier access to and utilization of the periphyton associated with the plant by grazers. As mentioned earlier fish predation on molluscs in Lake Kariba may be low, which may also account for greater proportions of gastropods on *Vallisneria*. Fisher (2005), using artificial plants, complex *Hydrilla*-like and simple *Vallisneria*-like plants, found that plant morphology had no significant effect on macroinvertebrate abundances, except for the densities of gastropod grazers, whose abundance was much greater on the simply-structured plants.

Both *Lagarosiphon* and *Vallisneria* were associated with similar and low abundances of filterer macroinvertebrates. Other studies have shown that the proportion of filterers in epiphytic macroinvertebrate communities tends to decrease with increase in microhabitat complexity (e.g., Cyr & Downing 1988b, Rennie & Jackson 2005). According to Carpenter & Lodge (1986) and Hamilton *et al*. (1990) low abundances of filterers associated with macrophytes are a result of decrease in suspended algal concentrations in macrophyte beds, which promote sedimentation of algae rather than its suspension in the water column, due to shading and reduction of water velocity or current.

Thus, there were differences in the functional assemblage of macroinvertebrate communities associated with the two macrophytes. The greater morphological complexity of *Lagarosiphon* was associated with a community skewed towards collector-gatherers, while on *Vallisneria*, collector-gatherers and grazers were equally important.

Diversity is positively associated with habitat complexity (Washington 1984, Downes *et al.* 1998). Habitat complexity has also been shown to affect species abundance and richness of fish (e.g., Charbonnel *et al.* 2002, Gratwicke & Speight 2005), and aquatic invertebrate assemblages (Beisel *et al.* 2000). This study shows that habitat complexity may not necessarily result in greater assemblage diversity and taxon richness. Although macroinvertebrate abundances tended to be greater on *Lagarosiphon* than on *Vallisneria*, the average number of taxa and diversity were not different, while evenness was significantly greater on *Vallisneria*. Evenness is a measure of proportional distribution of different taxa in a community and the less equitable the distribution the lower is the evenness. The slightly but significantly lower evenness of macroinvertebrate community associated with *Lagarosiphon* compared to *Vallisneria* was generally due to increased dominance of taxa such as Chironominae and Oligochaeta.

3.4.3 Size class distribution of chironomids and two mayfly genus associated with *Lagarosiphon* and *Vallisneria*

The size class distributions of chironomids and *Caenis* were not different between *Lagarosiphon* and *Vallisneria* (Figure 3.3). *Cloeon*, which is primarily a collector-gatherer, had a significantly greater proportion of large individuals on *Lagarosiphon*, while a greater proportion of larger individuals of the predatory coenagrionid naiads were found on *Vallisneria*. The initial expectation of this study was that size class distribution of macroinvertebrates would be biased towards larger sizes being associated with the more morphologically complex macrophyte. Fish predators are generally size-selective (Wahlström *et al.* 2000, Rettig 2003) but tend to be less effective in complex habitats (Swisher *et al.* 1998) due to the availability of greater number of refuges for prey. A greater proportion of large-sized *Cloeon* was therefore associated with *Lagarosiphon* possibly because structural complexity of the plant reduced its encounters with predators such as coenagrionid naiads and predatory fish. Intra-guild predation may have resulted in greater proportion of large coenagrionids being associated with *Vallisneria*. Large odonates are known to prey on smaller individuals (Robinson & Wellborn 1987) and so in a less complex environment intraguild predation may be higher compared to complex environments, which tend to diminish the predatory interactions. Thus higher levels of intraguild predation in the less morphological complex *Vallisneria* was one of the factors that possibly led to relatively fewer numbers of small sized coenagrionid naiads.

3.4.4 Conclusions

The findings of this study lend support to the theory that morphological complexity of macrophytes has an impact on epiphytic macroinvertebrate community structure (e.g. Cheruvelil *et al.* 2000, 2002). The two submerged macrophytes, *Lagarosiphon* and *Vallisneria*, present two contrasting habitat types to colonizing epiphytic macroinvertebrates in Lake Kariba. The long flat ribbon like leaves of *Vallisneria* offers a simpler habitat compared to the long filiform stems with many, alternate small leaves of *Lagarosiphon*. Although similar macroinvertebrate communities were associated with the two plant species, the greater morphological complexity of *Lagarosiphon* resulted in greater abundances of most taxa, likely due to the provision of better refuge from predation and high quantities of trapped particulate organic matter that are used as food by many invertebrates. The study thus to some extent supports the 'habitat heterogeneity hypothesis,' which postulates that highly complex habitats provide more niches, greater feeding opportunities and increased refugia from predation and are therefore associated with greater abundances and diversity of organism than simple habitats (Orth 1992, Tews *et al.* 2004).

Macroinvertebrate communities of lakes are an important link in the transfer of energy from primary producers and detritus to higher trophic levels. The differences in epiphytic communities associated with *Lagarosiphon* and *Vallisneria* may be important in functional or food web dynamics such that changes towards one or the other of the two macrophytes may have an effect on higher trophic levels in Lake Kariba and thus affect the overall fish species diversity and abundance.

Lagarosiphon is the most widespread and dominant submerged macrophyte and has a broader vertical distribution than most of the submerged species in Lake Kariba (Machena & Kautsky 1988). Comparing the results obtained in this study to those obtained by Bowmaker (1973) suggests that the widespread establishment of

Lagarosiphon in the lake has probably led to increased abundances of epiphytic macroinvertebrate taxa and in the total macroinvertebrate abundance. The greater macroinvertebrate abundances associated with *Lagarosiphon* compared to *Vallisneria* makes it a more valuable invertebrate food source for fish species. The possible decline in *Vallisneria* occurrence in the shallow inshore waters of Sanyati Basin observed between 2005 and 2008 was likely of no great consequence for submerged macrophyte associated macroinvertebrate abundance and diversity, and fish productivity.

This study showed that the same invertebrate taxa generally occurred on *Lagarosiphon* and *Vallisneria*, with much reduced numbers of virtually all taxa occurring on the later plant species. Because of this and the dominance of *Lagarosiphon* in Lake Kariba, I decided that I would focus on *Lagarosiphon* to study temporal aspects of the epiphytic invertebrates. In Chapters 4 and 5 I therefore present results of a weekly sampling programme that was carried out over a thirteen-month study period, of relationships between invertebrates associated with *Lagarosiphon* and water physicochemical variables.

CHAPTER 4

TEMPORAL VARIATION AND THE EFFECT OF WATER PHYSICOCHEMICAL CHARACTERISTICS ON MACROINVERTEBRATES ASSOCIATED WITH *Lagarosiphon*

4.1 Introduction

In lakes, physicochemical factors such as changes in water chemistry (Pagano & Titus 2004), ground water movement (Lodge *et al*. 1989), wave exposure, light penetration and substrate slope (Duarte & Kalff 1986), substrate type (Barko & Smart 1986) and water level fluctuations (Hellsten & Riihimäki 1996, Chow-Fraser *et al.* 1998, Hellsten 2000) are important in structuring submerged plant communities. Biotic factors that affect macrophytes include interspecific competition (Titus et *al.* 2004), invasions by exotic species (Madsen *et al.* 1991), disturbance, damage of macrophytes and re-suspension of sediments by fish such as the cyprinid, *Cyprinus carpio* (Lougheed *et al.* 1998, Chow-Fraser *et al.* 1998), herbivory (Lodge *et al.* 1998, Titus *et al.* 2004) and differences in life cycle patterns among different plant species (Collier 2004).

Temporal changes in invertebrate assemblages associated with macrophytes have also been shown to be driven by a variety of biotic and abiotic factors. The taxonomic diversity of macrophyte stands can influence macroinvertebrate assemblage structure (Brown *et al.* 1988). A number of studies (e.g., Chapter 3 of this thesis, Wissinger 1999, Bogut *et al*. 2007) have shown differences among different aquatic plant species in invertebrate species composition and abundance. This has largely been attributed to plant growth form or morphology, which affects habitat complexity and thus determining the level of protection from predators and amount of food available. Secondary plant metabolites in some freshwater plant species have also been shown to affect epiphytic macroinvertebrate structure (Bolser *et al.* 1998, Cronin 1998). Variations in macroinvertebrate (Collier 2004) and macrophyte (Hargeby 1990, Collier 2004) life cycles also affect macroinvertebrate assemblage structure. Seasonal die off of some macrophyte species during winter periods limits epiphytic invertebrates to plants that grow all year round (Hargeby 1990), while invertebrate communities associated with newly established macrophyte habitats are largely affected by differences in colonization rates between invertebrate species (Sheldon 1984). According to Hargeby (1990) the epiphytic invertebrate community structure in long lasting or permanent macrophyte beds are primarily determined by density-dependent animal interactions, while in new macrophyte habitats they are largely due to the colonization ability of different invertebrate species.

Temporal variation in physicochemical environmental conditions affects freshwater macroinvertebrate community structure (Mykrä 2006). A number of water bodies show seasonal variation in hydrology, with variation in water levels a key component in structuring invertebrate assemblages (Euliss *et al.* 2004). In temperate regions the marked seasonality in water temperatures is a major factor affecting invertebrate communities (Oertli 1995). Other abiotic factors that affect invertebrate assemblages include type of bottom substrate, chemical composition of water, light penetration, oxygen concentration and pH (Ward 1992).

Most studies of the temporal dynamics of macrophyte and invertebrate assemblages have been done on water bodies in temperate regions where patterns and processes may be markedly different from those in other environments. On Lake Kariba the temporal aspects of aquatic plants and epiphytic macroinvertebrate are largely unknown. The purpose of this study was to explore the temporal aspects of the macroinvertebrate community associated with *Lagarosiphon* in the shallow inshore waters of Lake Kariba. The study primarily focused on monthly changes in the macroinvertebrate community structure. The main objective was to explore the effect of seasonal variations in physical and chemical conditions in the water on the structure of the macroinvertebrate assemblage associated with *Lagarosiphon*.

4.2 Materials and Methods

This study was carried over a thirteen-month period, August 2007 to August 2008. Epiphytic invertebrate on *Lagarosiphon* and water samples were collected on a near weekly basis. In total 50 invertebrate samples were collected during the study period. A detailed description of the materials and methods used is given in section 2.3.2.

4.3 Results

4.3.1 Water chemistry

Weekly water physicochemical conditions at the sampling site during the study period are shown in Appendix 5 and monthly means in physicochemical conditions in Figure 4.1. Average water temperature for the study period ranged between 23.9^{O}C (July 2008) and 30.6^{O}C (February). There was a gradual increase in mean water temperature from August 2007 to February and a gradual decrease thereafter, with significant differences among some of the months (Kruskal-Wallis ANOVA, H = 39.80, df = 12, p < 0.01). Mean water temperatures in the period October to May were significantly greater than those in August 2007, June, July and August 2008 (Mann Whitney U test, p < 0.05).

The range in mean pH for the study period was 7.20 to 8.20, and significant differences occurred among months (Kruskal-Wallis ANOVA, H = 33.93, df = 12, p < 0.01). Comparatively low pH values were recorded in September and May (Figure 4.1), which were significantly less than most of the other months (Mann Whitney U test, p < 0.05). The mean conductivity was between 100 and 110 μS/cm from August 2007 to April, as well as in August 2008 (Figure 4.1). There was a slight rise in mean conductivity (110 – 120 μS/cm) in May to July. Turbidity also differed significantly during the study period (Kruskal-Wallis ANOVA, H = 34.40, df = 12, p < 0.01), with mean values recorded in November significantly greater than those recorded for January, March, June and July (Mann Whitney U test, p < 0.05). Dissolved oxygen concentrations differed significantly during the study period (ANOVA, $F_{12, 32}$ = 6.964, p < 0.001), with mean percent oxygen saturation in August 2007 significantly greater than in December as well as the period from February to July (Tukey Q test, p < 0.05). Mean percent oxygen saturation in October was significantly greater than in February, May, and July (Tukey Q test, p < 0.05), while the average oxygen saturation in May was significantly less than in November and January (Tukey Q test, p < 0.05).

The average total phosphorus (TP) concentrations differed significantly during the study period (ANOVA, $F_{8,\ 27} = 2.976$, $p = 0.016$), with mean concentration in August 2007 significantly greater than in February (Tukey Q test, $p < 0.05$). There were no significant differences in mean phosphorus concentration between any of the other months. The concentrations of total nitrogen (TN) varied significantly among months (ANOVA, $F_{9,\ 30} = 8.855$, $p < 0.01$), with mean concentration in November being significantly differently and greater than in April (Tukey Q test, $p < 0.05$). The concentrations of both ammonium (Kruskal-Wallis ANOVA, H = 18.22, df = 8, p = 0.02), and nitrates (Kruskal-Wallis, ANOVA, H = 19.29, $p = 0.0134$) also differed significantly among months. The average ammonium concentration in February was significantly greater than in August 2007, September, December and March (Mann Whitney U test, $p < 0.05$), while the nitrate concentration in December was significantly greater than in the period between August 2007 and April (Mann Whitney U test, $p < 0.05$). The mean concentration of phosphates did not differ significantly from August 2007 to April (ANOVA, $F_{8,\ 27} = 1.246$, $p = 0.312$). During the study period water levels in the lake decreased from August 2007 to December, after which levels were increasing up to July (Figure 4.1).

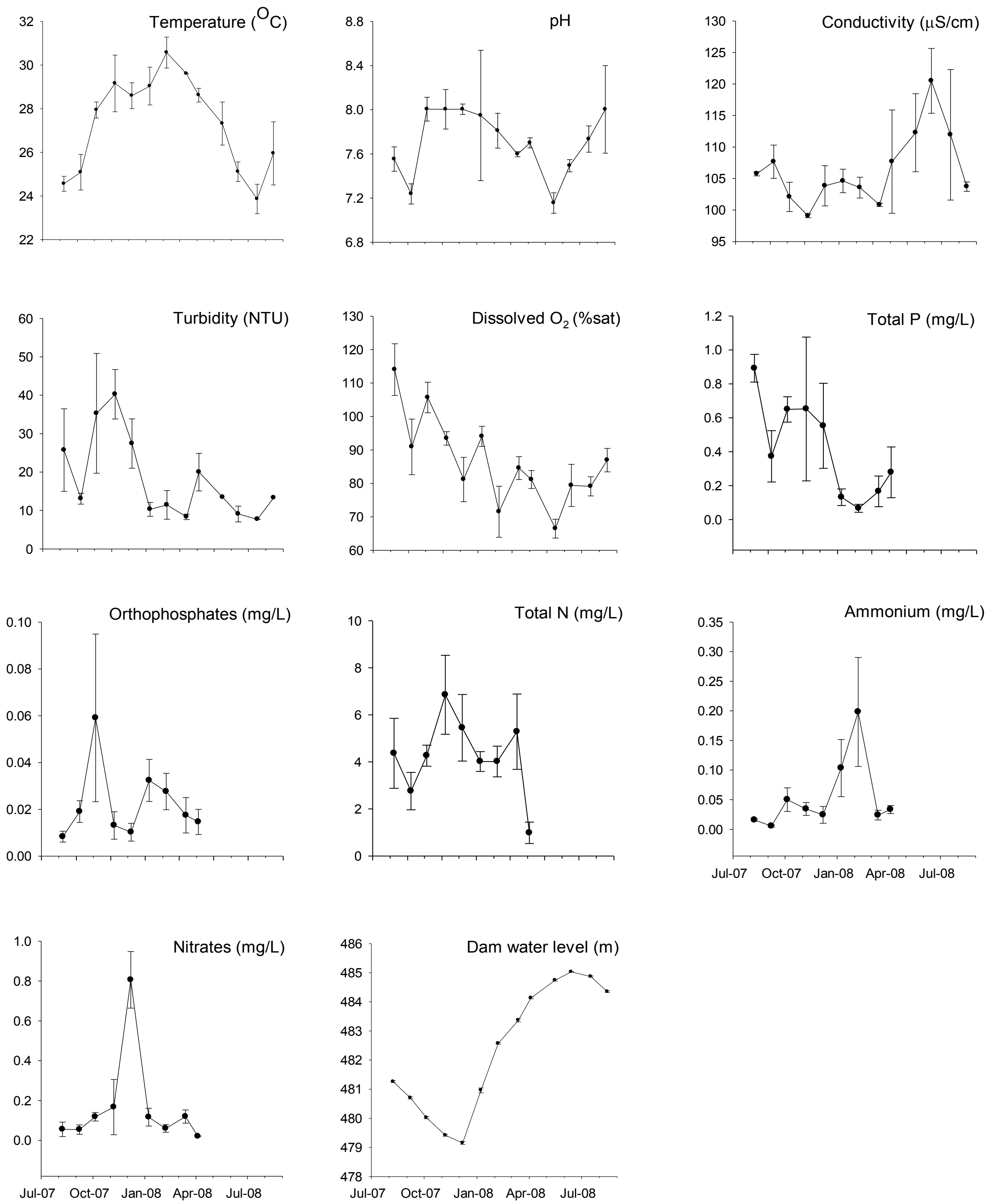

Figure 4.1. Variation in monthly means of water physicochemical parameters during the study period. Error bars are ±1 standard error. Note the differences in scale on the y axis of the graphs. The lake usually, de-stratifies in May/June and stratifies in August.

Table 4.1 shows the eigen values of the first five axes of the principal component analysis (PCA) of water physicochemical parameters. The five axes together accounted for 75% of the total variation in water physicochemical conditions. Water level showed strong positive correlation with the first principal axis (Appendix 6). Conductivity was also positively correlated with the first principal component, while temperature, pH, turbidity, percent oxygen saturation (% O), total phosphorus (TP), phosphates, total nitrogen (TN) and nitrates were negatively correlated with the first principal component. Water temperature and nitrate concentration were positively while turbidity, %O and TP negatively correlated with the second principal component (Appendix 6). The PCA ordination separated the environmental variables, suggesting temporal patterns in the water physicochemical characteristics. Appendix 7 which shows the principal component scores contributed by each sample collected during the study period to the five principal components of the PCA, shows distinct separation of the samples, especially on the first principal component. Physicochemical aspects from August 2007 to March were separated from those in the period from April to August 2008 along the first principal component (Appendix 7). The other principal components did not show a distinct temporal separation. Principal component analysis thus suggests that water level was a key aspect in temporal variation of water physicochemical conditions of shallow marginal waters of Lake Kariba. Figure 4.2 the hierarchical classification of normalised physicochemical characteristics also shows that there was separation of conditions at the site during the study period into five distinct groups, 1 (August 2007–October), 2 (October–December), 3 (January–April), 4 (April–June) and 5 (July–August 2008).

Table 4.1 Results of the principal components analysis of physicochemical data, showing the eigen values for the first five principal components as well as the percent of total variance contributed by each component.

PC	Eigen value	% Variation	Cum.%Variation
1	3.56	29.70	29.70
2	2.22	18.50	48.10
3	1.28	10.70	58.80
4	0.99	8.20	67.10
5	0.96	8.00	75.00

4.3.1.1 Relationships among water variables

Water temperature was significantly and negatively correlated with total phosphorus concentration (Spearman Rank correlation, r = -0.599, p < 0.001) and conductivity (r = -0.372, p = 0.012) and water level (r = -0.305, p = 0.041), but was positively correlated with ammonium concentration (Spearman Rank correlation, r = 0.415, p = 0.020) and pH (r = 0.342, p = 0.022). Dam water level was significantly and negatively correlated with nitrate (r = -0.381, p = 0.034) and dissolved oxygen concentration (r = -0.512, p < 0.001), pH (r = - 0.362, p = 0.015), and turbidity (r = 0.555, p < 0.001), but positively and significantly correlated with conductivity (r = 0.334, p = 0.025).

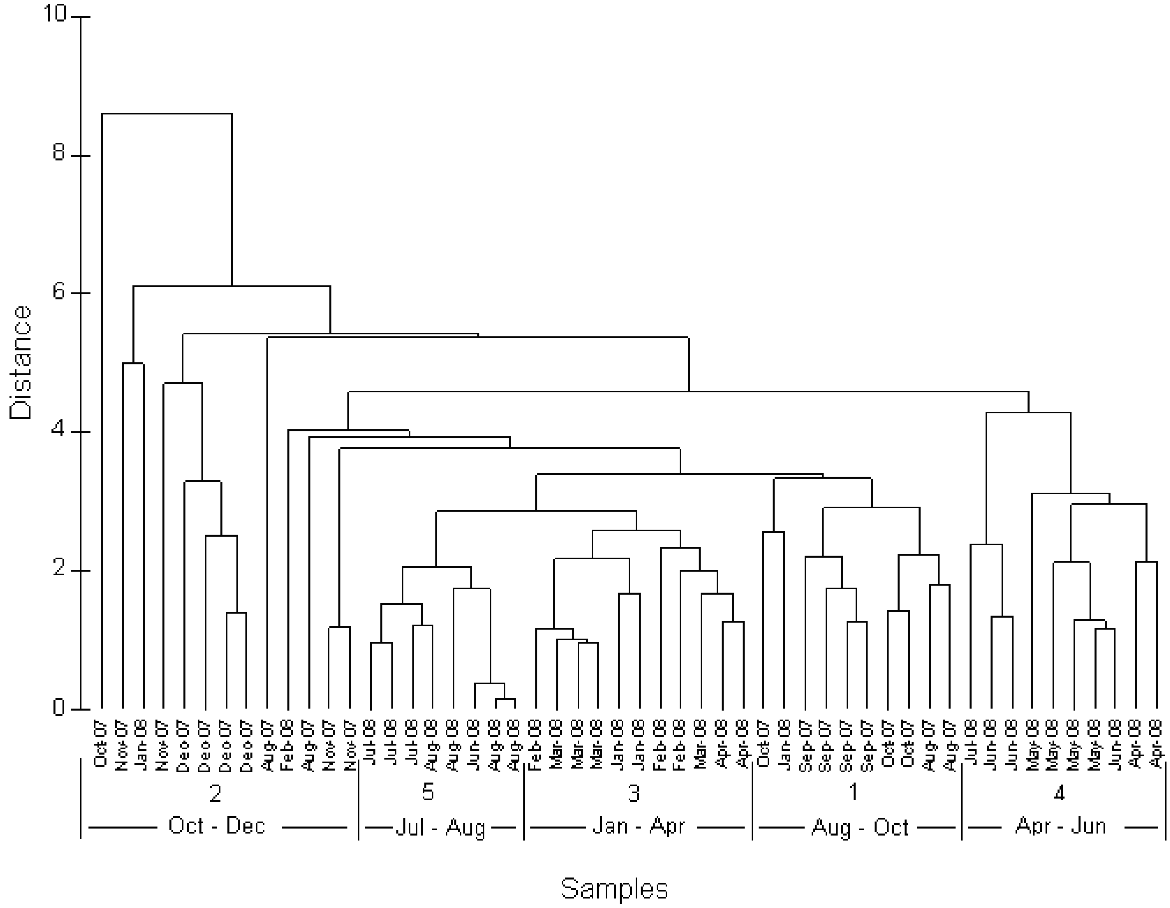

Figure 4.2. Hierarchical clustering of water samples from site 6 based on physicochemical conditions during the study period (August 2007 to August 2008).

4.3.2 Macroinvertebrates associated with *Lagarosiphon*

A total of 21 macroinvertebrate orders and 50 families were identified from the 50 samples that were collected during the 13-month study period (Table 4.2). The most frequently occurring taxa, *Dugesia* sp, Naididae, *Physa acuta*, Hydracarina, *Cyclestheria hislopi*, Ostracoda, *Caenis* sp, *Cloeon* sp, *Pseudagrion* sp, *Enallagma* sp, *Ischnura* sp, *Micronecta* sp, *Orthotrichia* sp, Chironominae, Tanypodinae and Orthocladiinae, all occurred in 70% or more of the samples and together contributed about 97% to the total number of organisms collected during the study. The most abundant non-insect taxa, *Dugesia*, Naididae, *P. acuta*, Hydracarina, *C. hislopi* and the Ostracoda altogether contributed 42.2% of the total number of macroinvertebrates. Of the insect taxa, the Chironomidae, which made up 39.2% of the total number of organisms, were largely dominated by Chironominae and Orthocladiinae. The other commonly occurring insect taxa, *Caenis, Cloeon*, *Pseudagrion*, *Enallagma*, *Ischnura*, *Micronecta*, and *Orthotrichia* contributed 15.6% to the total number of macroinvertebrates collected during the study (Table 4.2).

The overall mean abundance of Chironominae was significantly greater than all the other taxa (Mann Whitney U test, $p < 0.005$). The abundances of *Dugesia* and Naididae were significantly greater than all the other remaining taxa (Mann Whitney U test, $p < 0.05$).

Table 4.2. Macroinvertebrates associated with *Lagarosiphon* during the sampling period. Freq (%) = percent frequency of occurrence, RA (%) = relative percent abundance or contribution to the total number of invertebrates collected during the study. Abundance = number per gram dry mass of *Lagarosiphon.* [a]Denotes macroinvertebrates taxa identified to the Order, [b]Family and [c]Subfamily level of taxonomic separation. √ = present but values less than 0.01.

Order Family	Taxa	Freq. (%)	Abundance	RA (%)
Turbellaria				
Planariidae	*Dugesia* sp.	100	14.34 ± 2.09	11.65
Oligochaeta	Naididae[b]	100	12.63 ± 1.47	10.26
Rhynchobdellida				
Glossiphoniidae	*Alboglossiphonia* sp	44	0.18 ± 0.06	0.15
Gastropoda				
Lymnaeidae	*Lymnaea columella*	44	0.09 ± 0.02	0.07
Physidae	*Physa acuta*	98	1.82 ± 0.25	1.48
Planorbiidae	*Bulinus depressus*	52	0.17 ± 0.05	0.14
	Bulinus forskalii	32	0.09 ± 0.03	0.07
	Bulinus globosus	6	0.01 ± 0.00	0.01
	Bulinus sp.	36	0.14 ± 0.05	0.12
	Biomphalaria pfeifferi	6	√	√
Thiaridae	*Cleopatra nsedwensis*	64	0.27 ± 0.06	0.22
	Melanoides tuberculata	24	0.13 ± 0.08	0.11
Viviparidae	*Bellamya capillata*	16	0.02 ± 0.01	0.01
Hydrobiidae	*Lobogenes* sp.	4	0.01 ± 0.01	0.01
Ancylidae	*Ferrisia* sp.	72	0.67 ± 0.17	0.54
Pelecypoda	Sphaeriidae[b]	2	√	√
Hydracarina	Hydracarina	100	1.56 ± 0.18	1.27

Table 4.2. Continued

Order Family	Taxa	Freq. (%)	Abundance	RA (%)
Cladocera				
Bosminidae	*Bosmina* sp	2	√	√
Daphnidae	*Daphnia lumholtzi*	18	0.06 ± 0.03	0.05
	Daphnia sp	30	0.09 ± 0.03	0.08
	Ceriodaphnia sp.	50	0.30 ± 0.10	0.24
Sididae	*Diaphanosoma* sp.	4	0.03 ± 0.03	0.03
Chydoridae	*Chydorus* sp.	4	0.01 ± 0.01	0.01
	Camptocercus sp.	2	0.01 ± 0.01	0.01
	Dunhevedia sp.	2	√	√
	Eurycercus sp.	8	0.01 ± 0.01	0.01
Copepoda	Diaptomidae[b]	16	0.03 ± 0.01	0.02
Cyclopoida	Cyclopoida[a]	34	0.07 ± 0.02	0.06
Decapoda				
Atyidae	*Caridinia nilotica*	56	0.08 ± 0.03	0.06
Conchostraca				
Cyclestheriidae	*Cyclestheria hislopi*	72	2.40 ± 0.40	1.95
Ostracoda	Ostracoda[a]	100	19.16 ± 5.48	15.56
Collembola	Isotomidae[b]	10	√	√
	Poduridae[b]	2	√	√
	Sminthuridae[b]	6	0.01 ± 0.00	√
Ephemeroptera				
Caenidae	*Caenis* sp.	96	1.57 ± 0.26	1.27
Baetidae	*Cloeon* sp.	100	8.59 ± 1.03	6.98
	Acanthiops sp	2	√	√
Oligoneuriidae	*Elassoneuria* sp	2	√	√

Table 4.2. Continued

Order Family	Taxa	Freq. (%)	Abundance	RA (%)
Odonata				
Coenagrionidae	*Pseudagrion* sp.	98	1.04 ± 0.12	0.84
	Enallagma sp.	96	1.00 ± 0.13	0.81
	Ischnura sp.	98	1.28 ± 0.14	1.04
Aeshnidae	*Aeshna* sp.	6	0.01 ± 0.00	0.01
	Anax sp.	48	0.04 ± 0.01	0.03
Gomphidae	Gomphidae	6	0.01 ± 0.00	0.00
Libellulidae	*Bradinopyga* sp	36	0.05 ± 0.02	0.04
	Orthetrum sp	2	√	√
	Tetrathemis sp	2	√	√
	Trithemis sp	12	0.01 ± 0.00	0.01
	Libellulidae[b]	32	0.07 ± 0.02	0.05
Hemiptera				
Belostomatidae	*Appasus* sp.	52	0.04 ± 0.01	0.03
Corixidae	*Micronecta* sp.	94	4.29 ± 0.79	3.48
Gerridae	*Hynesionella* sp.	2	0.00 ± 0.00	0.00
	Eurymetra	16	0.08 ± 0.04	0.07
	Rhagadotarsus	18	0.03 ± 0.02	0.03
Mesovelidae	*Mesovelia*	16	0.02 ± 0.01	0.02
Naucoridae	Naucoridae	2	√	√
Nepidae	*Ranatra* sp.	20	0.01 ± 0.00	0.01
Notonectidae	*Anisops* sp.	36	0.12 ± 0.04	0.10
	Enithares sp.	32	0.05 ± 0.02	0.04
Pleidae	*Plea* sp.	36	0.04 ± 0.01	0.03
Lepidoptera	Nymphulinae	4	√	√
Homoptera	Aphididae	20	0.02 ± 0.01	0.02

Table 4.2 Continued

Order Family	Taxa	Freq. (%)	Abundance	RA (%)
Coleoptera	Dysticidae[b]	60	0.06 ± 0.01	0.05
	Hydraenidae	2	√	√
Hydrophilidae	*Helophonis* sp.	2	√	√
	Hydrophilidae	6	0.02 ± 0.01	0.02
Curculionidae	*Neochetina* sp.	26	0.02 ± 0.01	0.02
Chrysomelidae	Chrysomelidae	4	√	√
Trichoptera				
Hydroptilidae	*Orthotrichia* sp.	100	1.43 ± 0.22	1.16
Ecnomidae	*Ecnomus* sp.	56	0.06 ± 0.02	0.05
Leptoceridae	*Leptocerina* sp.	2	√	√
	Athripsodes sp.	4	0.01 ± 0.01	0.01
Diptera				
Ceratopogonidae	*Bezzia* sp.	40	0.05 ± 0.02	0.04
Chaoboridae	*Chaoborus* sp.	18	0.01 ± 0.00	0.01
Chironomidae	Chironominae[c]	100	38.75 ± 8.35	31.49
	Tanypodinae[c]	90	0.51 ± 0.14	0.42
	Orthocladiinae[c]	100	8.99 ± 1.82	7.30
Culicidae	*Anopheles* sp.	18	0.02 ± 0.01	0.02
	Culex	2	√	√
	Malaya sp.	4	0.01 ± 0.01	0.01
	Mansonia sp.	2	√	√
Dolichopodidae	Dolichopodidae[b]	2	√	√
Simulidae	Simulidae[b]	2	√	√
Stratiomyidae	Stratiomyidae[b]	8	0.03 ± 0.03	0.03
Tabanidae	Tabanidae[b]	2	√	√
Tipulidae[b]	Tipulidae[b]	10	0.07 ± 0.05	0.06
Unidentified		18	0.24 ± 0.12	0.20

4.3.3 Temporal variation of common macroinvertebrate taxa

The temporal variations in mean abundances of the common taxa that occurred on *Lagarosiphon* are shown in Figure 4.3.

4.3.3.1 Turbellaria

Between August 2007 and February the mean abundance of *Dugesia* sp. gradually decreased, but underwent a steady increase thereafter (Figure 4.3a). *Dugesia* abundances were significantly different among months (ANOVA, $F_{12, 39} = 25.21$, $p < 0.001$). The greatest numbers were obtained in July and August 2008 (Figure 4.3a). The mean abundance of *Dugesia* in August 2008 was significantly greater than in all the other months (Tukey Q test, $p < 0.05$) except July (Tukey Q = 3.065, $p = 0.619$), while in July the abundance was significantly greater than the other remaining months (Tukey Q test, $p < 0.05$) except August 2007 and September (Tukey Q = 3.706, $p = 0.333$). The average abundances in August 2007 and September were also significantly greater than in November, and the period January to June (Tukey Q test, $p < 0.05$), while abundances obtained from January to April were significantly less than in October (Tukey Q, $p < 0.05$).

4.3.3.2 Naididae

Three peaks, in August 2007, February and August 2008, were observed in the mean abundance of the Naididae (Figure 4.3a), with significant differences recorded during the study period (ANOVA, $F_{12, 39} = 7.001$, $p < 0.001$). The mean abundance of naidids in July and August 2008 were significantly greater than in November, December, May and June, while abundances in August 2007 and September were significantly greater than in November and June (Tukey Q, $p < 0.05$). June abundances were also significantly less than in October and February (Tukey Q, $p < 0.05$).

4.3.3.3 Gastropoda

Seven gastropod families were associated with *Lagarosiphon* (Table 4.2). The four most frequently occurring families, which occurred in more than 50% of the samples, were Physidae, Planorbiidae, Thiaridae and Ancylidae. The physid, *Physa acuta*, was the most frequent and abundant gastropod taxon (Table 4.2). The abundance of *P.*

acuta was relatively steady and did not differ significantly from August 2007 to November (Kruskal-Wallis ANOVA, $p > 0.05$). Relatively high abundances were obtained in December, January and August 2008 and low abundances occurred from February to July (Figure 4.3a). The mean abundance in December was significantly greater than those from August to October, and from February to July, while abundances in January and August 2008 were significantly greater than in February to July (Mann Whitney U test, $p < 0.05$). In August 2008 the mean abundance of *P. acuta* was also significantly greater compared to abundances in September and October (Mann Whitney U test, $p < 0.05$). Generally, mean abundances of *P. acuta* from February to July 2008 were significantly less compared to all the other months (Mann Whitney U test, $p < 0.05$).

4.3.3.4 Hydracarina and Conchostraca

The abundance of water mites (Hydracarina) was relatively constant throughout the study period (Figure 4.3a), and no significant differences were recorded (ANOVA, $F_{12, 39} = 0.984$, $p = 0.480$). During the first 5 months of the study, there were relatively low abundances of *C. hislopi*, but as of January its mean abundance increased and peak abundance was obtained in May (Figure 4.3a). There were no significant differences in abundance of *C. hislopi* from August 2007 to December (Kruskal-Wallis ANOVA, $p > 0.05$). In May the mean abundance was significantly greater than in all the other months (Mann Whitney U test, $p < 0.01$) except April (Mann Whitney U test, $p > 0.05$). The mean abundances of *C. hislopi* from January to August 2008 were significantly greater than those obtained in August 2007 to December (Mann Whitney test, $p < 0.05$).

4.3.3.5 Ostracoda

The mean abundance of Ostracoda showed significant temporal differences during the study period (Kruskal-Wallis ANOVA, H = 43.0, df = 12, $p < 0.01$). Numbers were relatively constant between August 2007 and December, decreased but maintained constantly low abundances between January and June, and increased in July and August 2008 (Figure 4.3b). The mean abundance obtained in August 2008 was significantly greater than those obtained in the other twelve months (Mann Whitney U test, $p < 0.05$). There were no significant differences in mean abundance from August 2007 to December (Mann Whitney U test, $p > 0.05$). Mean abundances in August 2007, October, November and July were significantly greater than those in January, February, April and May, while September and December abundances were significantly greater than in May (Mann Whitney U test, $p < 0.05$).

4.3.3.6 Ephemeroptera

Four ephemeropteran taxa, one caenid, *Caenis*, two baetids, *Cloeon* and *Acanthiops* and one oligoneurid, *Elassoneuria* occurred on *Lagarosiphon*. *Acanthiops* and *Elassoneuria* were not common and occurred in fewer than 5% of the samples. Relatively large numbers of *Caenis* were obtained in August 2007, September, October, July and August 2008 (Figure 4.3b), which were generally significantly greater than those collected from November to June (Kruskal-Wallis ANOVA, H = 43.37, df = 12, $p < 0.01$). There were no significant differences in mean abundances of *Caenis* between August 2007, September, October, July and August 2008 (Mann Whitney U test, $p > 0.05$). The mean abundances of *Caenis* in August 2007, September, October, July and August 2007 were significantly greater compared to abundances in November, January, February, April and May, while the mean abundance in August 2008 was also significantly greater than in December, March and June (Mann Whitney U tests, $p > 0.05$).

The lowest mean abundance of *Cloeon* was obtained in June 2008 and the highest in July 2008 and mean numbers were significantly different among some of the months (ANOVA, $F_{12, 39} = 8.567$, $p < 0.01$). Mean abundances in July and August 2008 were significantly greater than those from August 2007 to December (Tukey Q, $p < 0.05$). The abundance in July was also significantly greater than in March, April and June, while in August 2008 it was significantly greater than in March (Tukey Q, $p < 0.05$). There were also significantly greater abundances of *Cloeon* in May compared to November and June, while in June the abundance was significantly lower than in January, February and May (Tukey Q, $p < 0.05$).

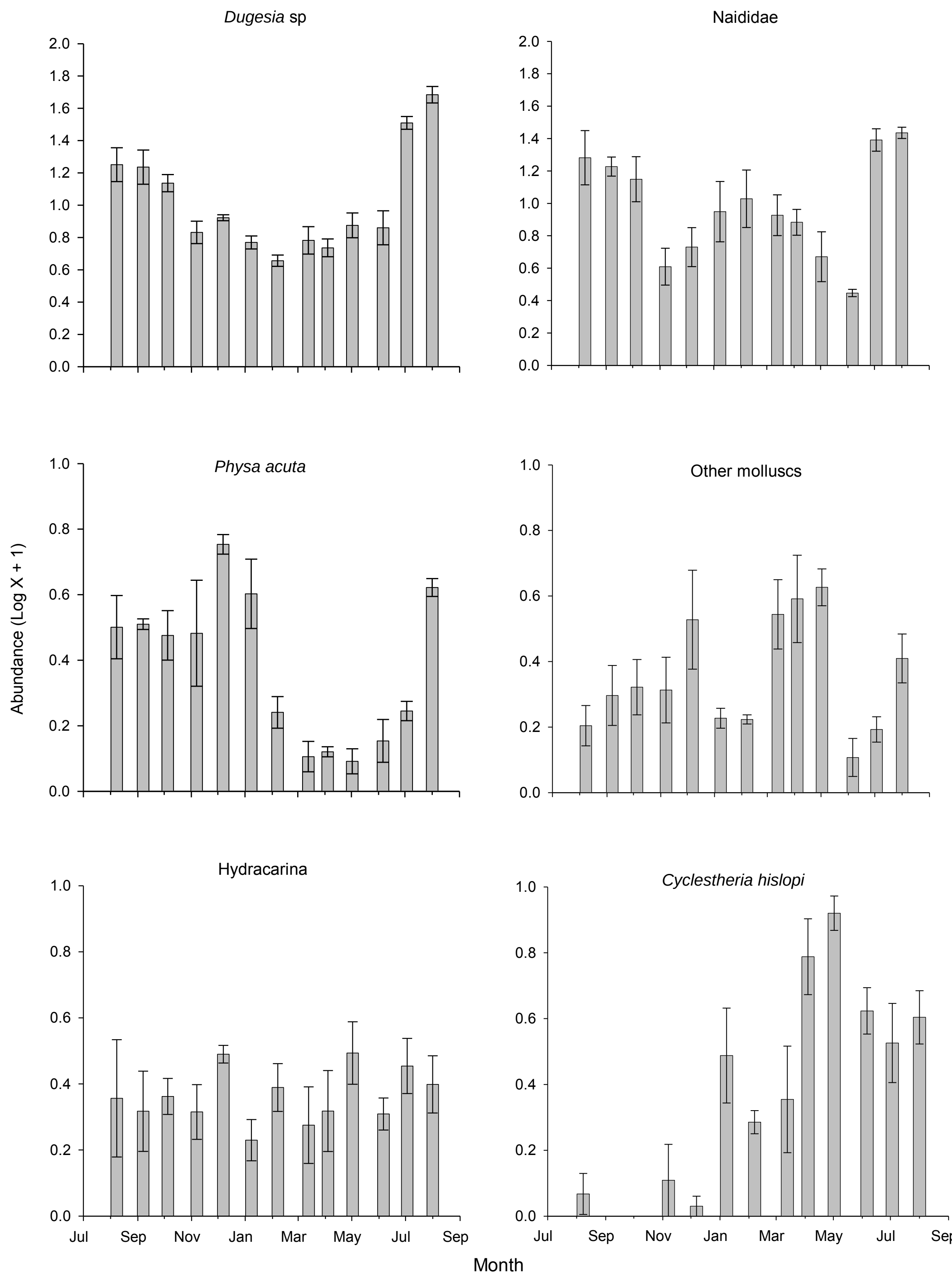

Figure 4.3a. The mean abundances (log x + 1) of the common and most abundant macroinvertebrate taxa associated with *Lagarosiphon***. Error bars represent ± 1 SE. Note the differences in scale on the y axis of the graphs**.

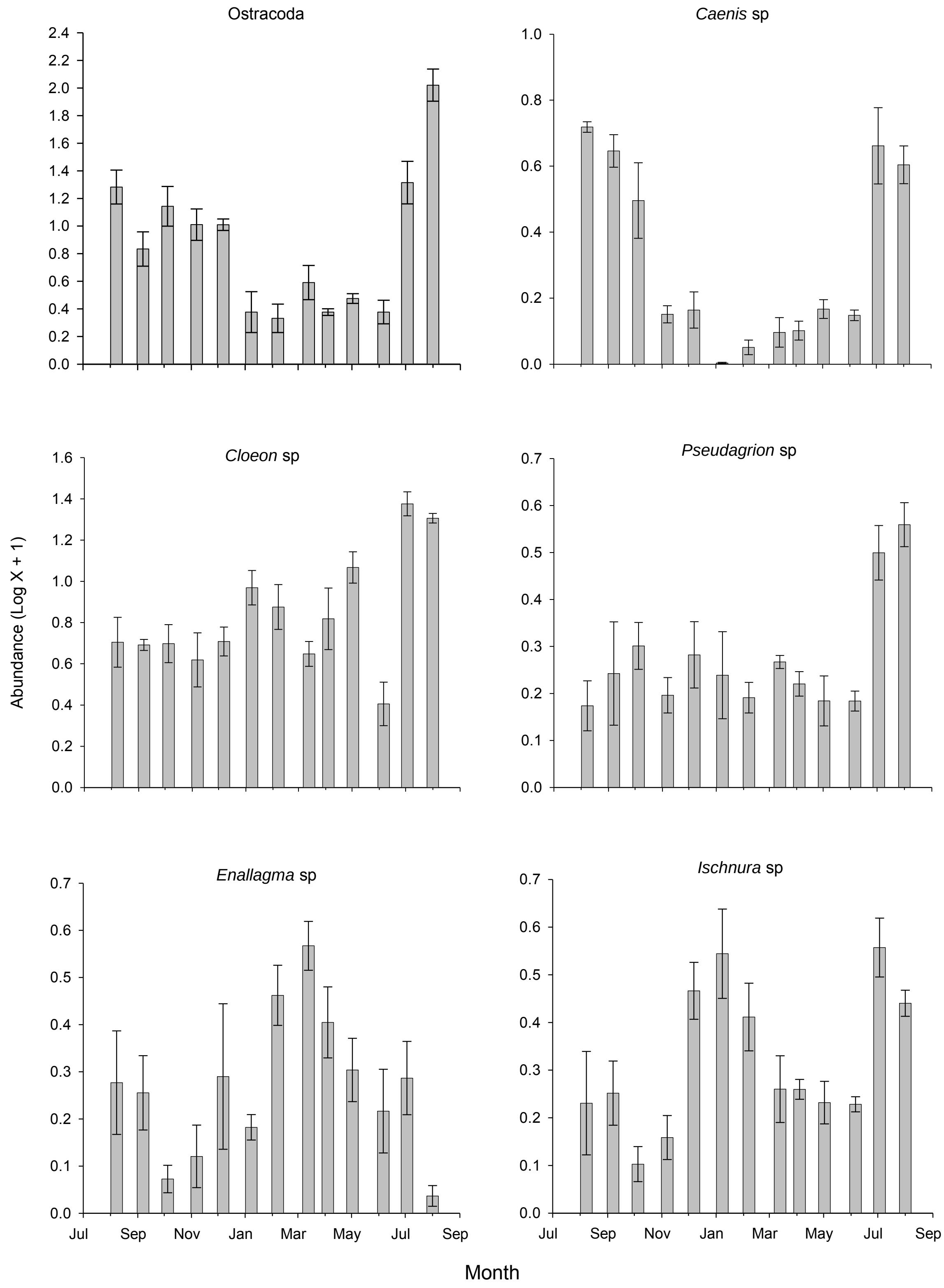

Figure 4.3b. The mean abundances of the common macroinvertebrate taxa associated with *Lagarosiphon*. Error bars represent ± 1 SE. Note the differences in scale on the y axis of the graphs.

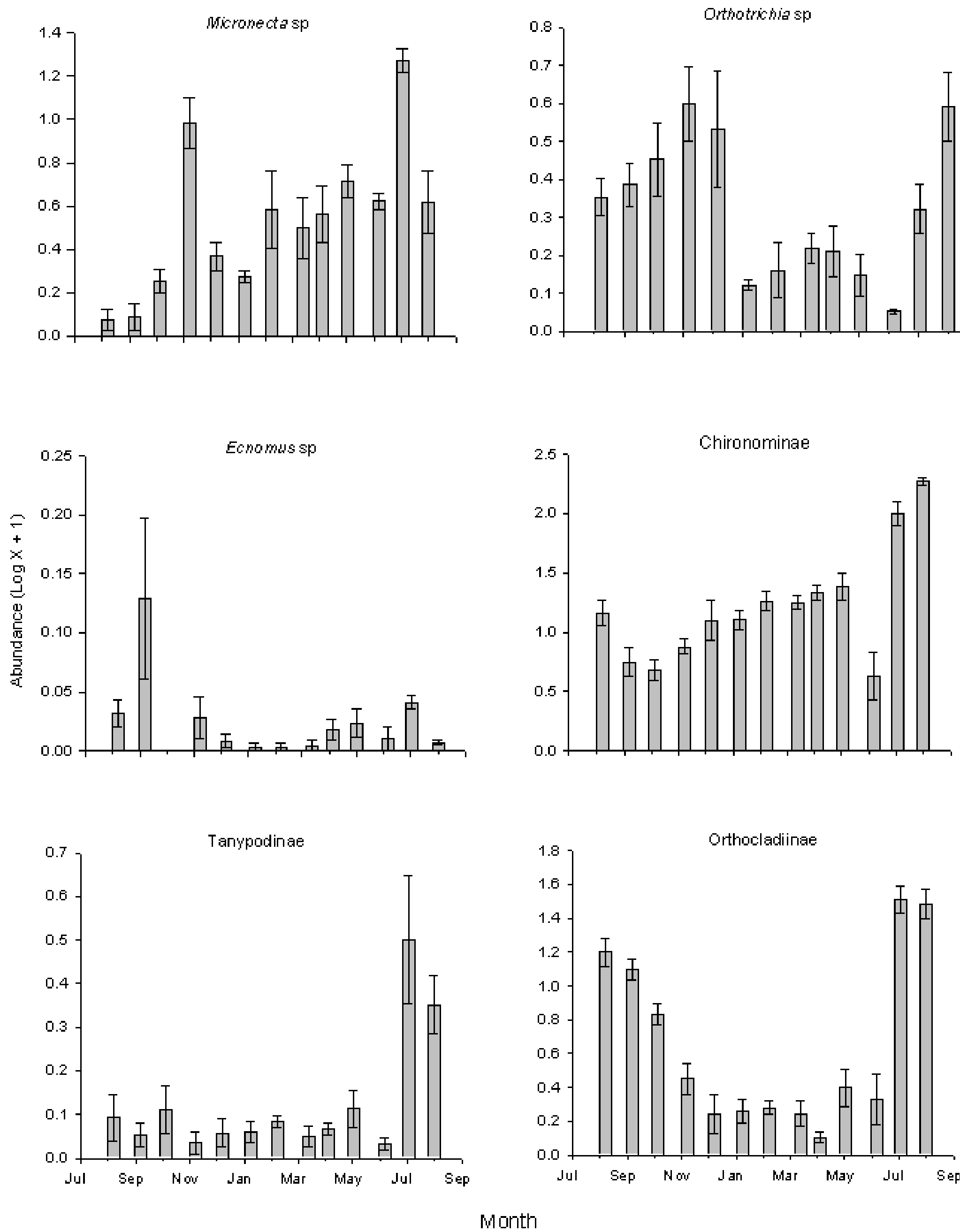

Figure 4.3c. The mean abundances (log X + 1) of the common and most abundant macroinvertebrate taxa associated with *Lagarosiphon***. Error bars represent ± 1 SE. Note the differences in scale on the y axis of the graphs**.

4.3.3.7 Odonata

Three damselfly taxa, *Pseudagrion*, *Enallagma* and *Ischnura*, occurred frequently on *Lagarosiphon* and there were no differences in overall mean abundances between the three taxa (Mann Whitney U test, $p > 0.05$). The abundance of all three taxa differed significantly among months during the study period (Kruskal-Wallis ANOVA, $p < 0.05$). From August 2007 to June there were no significant differences in mean abundance of *Pseudagrion* (Mann Whitney U test, $p > 0.05$). In August 2008 the mean abundance of *Pseudagrion* was significantly greater compared to those recorded in the period August 2007 to June, while the abundance in July was significantly greater than in the period August 2007 to November, as well as those in January, February, April and May (Mann Whitney U test, $p < 0.05$).

In the period between August 2007 to March, the mean abundance of *Enallagma* generally increased, but decreased thereafter (Figure 4.3b). The lowest mean abundance of *Enallagma* was obtained in August 2008, which was significantly less compared to August 2007, September, January to May and July (Mann Whitney U tests, $p < 0.05$). A low mean abundance of *Enallagma* was also obtained in October, which was significantly less compared to August 2007, January, February, April and July. The mean abundance of *Ischnura* generally decreased between August 2007 and November, rose sharply in December and January, then underwent a gradual decrease from February to June, and increased sharply in July/August 2008 (Figure 4.3b). The lowest mean numbers of *Ischnura* were collected in September and October, both of which were significantly lower than in January, February, April, July and August 2008 (Mann Whitney U test, $p < 0.05$). The relatively low abundances in April and May were significant less compared to those in January, July and August 2008 (Mann Whitney U test, $p < 0.05$). In August 2008 mean abundance of *Ischnura* was significantly greater than those obtained in June and July (Mann Whitney U test, $p < 0.05$).

4.3.3.8 Hemiptera & Trichoptera

Eleven hemipteran taxa occurred on *Lagarosiphon* but only one, the corixid *Micronecta*, was common and made a significant contribution to the number of organisms collected during the study. The other ten taxa contributed less than 1% to the overall total number of organisms. Two major peaks in mean abundances of *Micronecta*, were observed, in November and July, but generally mean abundances gradually rose during the study period (Figure 4.3c). The abundances of *Micronecta* in November and July were significantly greater compared to the other months of the study period (Mann Whitney U test, $p < 0.05$).

Three trichopteran taxa were collected from *Lagarosiphon*. The hydroptilid *Orthotrichia*, was present in all samples and on average made up 1.9% of the total number of individuals in each sample. The mean abundance of *Orthotrichia* underwent a gradual increase between August 2007 and December (Figure 4.3c) and was drastically reduced from January to June, but sharply increased in July and August 2008. In the period August 2007 to December there were no significant differences in mean abundance of *Orthotrichia* (Mann Whitney U test, $p < 0.05$). Generally, mean abundances from August 2007 to December and August 2008 were significantly greater than those obtained in January to June (Mann Whitney U test, $p < 0.05$). The ecnomid *Ecnomus* occurred in 56% of the samples and there were no significant differences in mean abundances between most months (Mann Whitney U test, $p > 0.05$), but the mean abundance in June was significantly greater than in October, while abundance in July was greater than in October, January, February and July (Mann Whitney U test, $p < 0.05$). The other two trichoptera, the leptocerids *Leptocerina* and *Athripsodes*, both occurred infrequently and in low abundances.

4.3.3.9 Diptera

The Diptera contributed 39.6% to the total number of organisms on *Lagarosiphon*. The most frequent and abundant dipterans were the chironomids. The chironomid subfamily Chironominae, which made up 31.5% of the total number of organisms collected during the study, was the most dominant taxa associated with *Lagarosiphon*. Its overall mean abundance for the study period was 38.8 ± 8.4 organisms per gram dry mass of *Lagarosiphon* and its highest mean abundances of 184.1 and 107.2 were obtained in August 2008 and July respectively. Between August 2007 and June, comparatively low abundances ranging between 4.05 and 30.42 were recorded, which were significantly lower than those in July and August 2008 (ANOVA, $F_{12, 39} = 22.67$, $p < 0.001$; Tukey Q test, $p < 0.05$). The mean abundance of Chironominae in May was also significantly greater than in September, October, November and June (Tukey Q test, $p < 0.05$). Abundances in February, March and April were all significantly greater than those in September, October and June (Tukey Q test, $p < 0.05$). In June significantly less numbers of Chironominae were also obtained than in August 2007, December and January, with October also having significantly lower abundance than August 2007 (Tukey Q test, $p < 0.05$).

Although occurring frequently the mean relative percent contribution to number of organisms in each sample by Tanypodinae was only 0.36%. Mean abundance for Orthocladiinae ranged from 0.3 ± 0.2 in April to 32.9 ± 10.5 in July and there were significant differences (ANOVA, $F_{12, 39} = 18.60$, $p < 0.001$) among months. From August 2007 to December mean abundance gradually decreased, was relatively unchanged between December and June, and rose sharply in July/August (Figure 4.3c). Significantly greater mean abundances of Orthocladiinae were obtained in August 2007, July and August 2008, than in the period from November to June (Tukey Q, $p < 0.05$). The abundance in September was also significantly greater than in period from December to June (Tukey Q test, $p < 0.05$), while in December, January, March and April abundances were significantly lower than in October, with April abundances also significantly less than in November and May (Tukey Q test, $p < 0.05$).

4.3.4 Temporal variation in total macroinvertebrate abundance

The range in mean total macroinvertebrate abundance on *Lagarosiphon* during the study period was between 30.2 ± 4.9 in June and 474.3 ± 29.7 in August 2008 (Figure 4.4), and significant differences were recorded among some of the months (ANOVA, $F_{12, 39} = 33.30$, $p < 0.01$). The mean macroinvertebrate abundances in July and August 2008 were significantly greater compared to any of the other months (Tukey Q test, $p < 0.001$). In August 2007 mean macroinvertebrate abundance was significantly greater than in November, January, February, March and June (Tukey Q test, $p < 0.05$). The total mean macroinvertebrate abundance in June was also significantly less than in September, October, December, February, April and May. The overall mean macroinvertebrate abundance on *Lagarosiphon* generally decreased between August 2007 and March, rose slightly in April and May, decreased sharply in June and sharply increased July and August 2008 (Figure 4.4). This was the general temporal pattern in abundance observed by most of the macroinvertebrate taxa associated with *Lagarosiphon*.

4.3.5 Relationships among invertebrate taxa

Analysis of relationships in the abundances of the main macroinvertebrate taxa on *Lagarosiphon* showed that the relationships among a considerable number of taxa were positive and significant (Spearman Rank correlation, $p < 0.05$) (Table 4.3). Out of a total of 136 pairwise comparisons, 56 (or 41.2%) were positively and significantly correlated, while only 8 (or 5.9%) were negatively and significantly correlated. Of the negative correlations, *Enallagma* was negatively and significant correlated with *Dugesia*, *P. acuta*, Ostracoda, *Orthotrichia* and Orthocladiinae, while *P. acuta* was negatively and significantly correlated with *C. hislopi*, *Micronecta* and *Orthotrichia*. Ten taxa, *Dugesia*, Oligochaeta, Ostracoda, *Caenis*, *Cloeon*, *Pseudagrion*, *Enallagma*, Chironominae, Tanypodinae and Orthocladiinae showed positive and significant correlations with five or more other taxa (Table 4.3).

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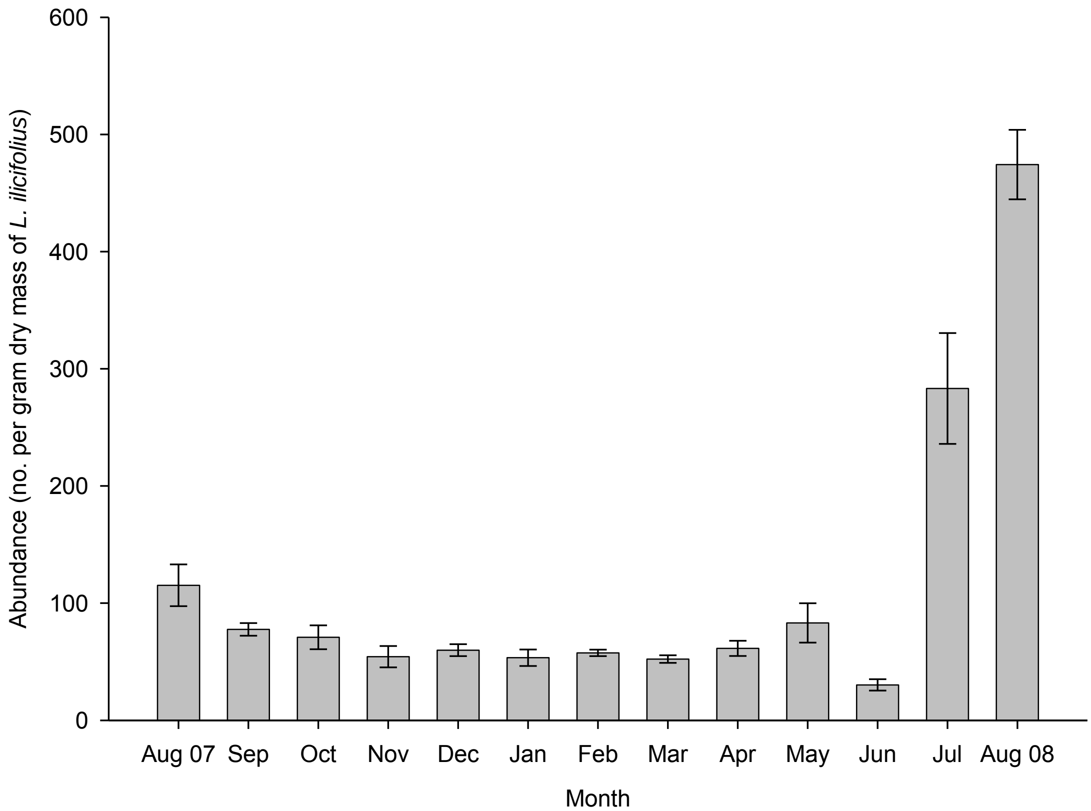

Figure 4.4. Temporal variation in macroinvertebrate abundance associated with *Lagarosiphon* during the study period.

Table 4.3. Spearman correlation coefficients [a] for the relationship in the abundance of the main invertebrate taxa associated with *Lagarosiphon* in Lake Kariba

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. *Dugesia*																
2.Oligochaeta	**0.65**															
3. *P. acuta*	**0.41**	**0.32**														
4. Acari	0.26	0.16	0.09													
5. *C. hislopi*	-0.17	-0.10	**-0.49**	0.06												
6. Ostracoda	**0.80**	**0.56**	**0.54**	**0.32**	-0.28											
7. *Caenis*	**0.73**	**0.53**	0.18	0.13	-0.21	**0.72**										
8. *Cloeon*	**0.29**	**0.39**	0.07	**0.29**	**0.42**	**0.29**	0.19									
9. *Pseudagrion*	**0.52**	**0.51**	0.05	0.17	0.20	**0.41**	**0.32**	0.26								
10. *Enallagma*	**-0.29**	0.00	**-0.48**	-0.00	0.18	**-0.43**	-0.26	-0.15	-0.08							
11. *Ischnura*	0.12	**0.34**	0.09	0.15	**0.34**	0.03	-0.01	**0.59**	0.26	0.11						
12. *Micronecta*	-0.03	-0.14	**-0.30**	0.13	**0.40**	-0.00	-0.11	**0.29**	0.13	0.00	0.06					
13. *Orthotrichia*	**0.48**	**0.39**	**0.47**	0.04	**-0.42**	**0.65**	**0.52**	-0.01	0.13	**-0.37**	-0.15	0.05				
14. *Ecnomus*	**0.32**	0.17	0.05	-0.09	-0.06	0.20	**0.32**	0.01	0.05	0.03	-0.06	0.18	0.19			
15. Chironominae	0.26	**0.35**	-0.09	0.05	**0.50**	0.18	0.10	**0.66**	**0.39**	0.13	**0.52**	**0.33**	-0.03	0.26		
16. Tanypodinae	**0.42**	**0.53**	0.05	0.04	0.23	**0.40**	**0.36**	**0.61**	**0.42**	-0.19	0.25	0.24	0.10	**0.29**	**0.61**	
17. Orthocladiinae	**0.85**	**0.69**	**0.34**	0.21	-0.17	**0.77**	**0.78**	**0.39**	**0.43**	**-0.31**	0.16	0.00	**0.43**	0.29	0.27	**0.46**

[a] Significant correlations ($P < 0.05$) are presented in bold type

4.3.6 Relationships between macroinvertebrate taxa and physicochemical variables

Table 4.4 shows the correlation between the most common and abundant macroinvertebrate taxa, as well as the overall macroinvertebrate abundance, with physicochemical variables measured during the study period. Seven taxa were significantly correlated with total phosphorus (TP) concentration (Spearman Rank correlation, $p < 0.05$). The abundances of *Dugesia*, Ostracoda, *Caenis*, *Orthotrichia* and Orthocladiinae were positively and significantly, while those of *C. hislopi*, and *Micronecta* were significantly and negatively correlated with TP concentration (Spearman Rank correlation, $p < 0.05$). The overall macroinvertebrate abundance also increased significantly with increase in concentration of TP (Spearman Rank correlation, $p < 0.05$). An increase in the concentration of phosphate (PO_4^{3-}) was associated with significant decreases in the abundances of Ostracoda and *Caenis,* as well as in the overall abundance of macroinvertebrates (Spearman Rank correlation, $p < 0.05$). Variation in the concentration of total nitrogen was not significantly correlated with abundance of any of the common invertebrates on *Lagarosiphon* (Spearman Rank correlation, $p > 0.05$). Ammonium concentration was significantly and negatively correlated with the abundances of *Dugesia*, *Caenis*, *Orthotrichia*, and the overall abundance of macroinvertebreates (Spearman Rank correlation, $p < 0.05$). The gastropod *P. acuta* and water mites were positively correlated while the trichopteran *Ecnomus* was negatively correlated with the concentration of nitrates. Thus relatively high total phosphorus concentrations were associated with high total invertebrate abundances, while high phosphate and ammonium concentrations were associated with low total invertebrate abundances.

Water pH was positively and significantly correlated with *P. acuta*, Ostracoda and *Orthotrichia*, and was negatively and significantly correlated with *C. hislopi* and *Enallagma* (Spearman Rank correlation, $p < 0.05$). The abundances of *Dugesia*, Naididae, Ostracoda, *Caenis*, *Pseudagrion*, *Ecnomus*, and Orthocladiinae, as well as total macroinvertebrate abundance were negatively and significantly correlated with water temperature (Spearman Rank correlation, $p < 0.05$). Figure 4.5 shows the variation with temperature in the abundances of the common invertebrate taxa associated with *Lagarosiphon*. The largest numbers of *Dugesia*, Naididae, Ostracoda, *Caenis*, *Pseudagrion*, Tanypodinae and Orthocladiinae were generally obtained at temperatures that were below 28^{O}C, with water temperatures greater than 30^{O}C characterised by greatly reduced numbers (Figure 4.5a & b). The total abundances of gastropods, odonates, hemipterans and trichopterans were not significantly correlated with temperature (Spearman Rank correlation, $p > 0.05$), while the total abundances of planariids, naidids ostracods, ephemeropterans and dipterans were significantly reduced at water temperatures greater than 28^{O}C compared to temperatures less than 28^{O}C (Spearman Rank correlation, $p < 0.05$).

The concostracan *C. hislopi* was significantly and positively correlated with conductivity (Spearman Rank correlation, $p < 0.05$). Water turbidity, negatively and significantly affected the abundances of Naididae, *C. hislopi*, *Ischnura*, Chironominae and Tanypodinae, but was positively and significantly correlated with *Orthotrichia* abundance (Spearman Ran correlation, $p < 0.05$).

The abundances of *P. acuta*, Ostracoda and *Orthotrichia* were positively and those of Acari, *C. hislopi*, *Enallagma*, *Micronecta* and Chironominae negatively and significantly correlated with dissolved oxygen concentration (Spearman Rank correlation, $p < 0.05$). The abundance of seven taxa, *C. hislopi*, *Cloeon*, *Pseudagrion*, *Ischnura*, *Micronecta*, Chironominae and Tanypodinae, increased significantly with increase in dam water levels, while *P. acuta* and *Orthotrichia* significantly decreased (Spearman Rank correlation, $p < 0.05$). Generally, significantly low abundances of gastropods (Spearma Rank correlation, r = -0.363, $p = 0.010$) and trichopterans (r = -0.439, $p = 0.001$) were associated with high water levels. The numbers of ephemeropterans (r = 344, $p = 0.014$), hemipterans (r = 0.448, $p = 0.001$) and dipterans (r = 0.426, $p = 0.002$) all significantly increased at high water levels. Overall, the total number of macroinvertebrate on *Lagarosiphon* was not significantly correlated with change in water level (Spearman Rank correlation, $p > 0.05$).

Thus generally, total macroinvertebrate abundance decreased at relatively high in concentrations of phosphates and ammonium. High water temperatures were also associated with significantly low numbers of various macroinvertebrate taxa as well as with low overall macroinvertebrate abundance, while high water levels were significantly associated with high numbers of various macroinvertebrate taxa but did not significantly affect total macroinvertebrate abundances associated with *Lagarosiphon*.

4.3.7 Univariate analysis of macroinvertebrate community structure

The average number of taxa associated with *Lagarosiphon* during the study period ranged between 23.8 ± 0.9 in October and 32.5 ± 1.2 in January (Figure 4.6a). The number of taxa differed significantly among some of the months (ANOVA, $F_{12, 39} = 3.246$, $p = 0.003$). The average number of taxa recorded in October was significantly less than in December, January, and April, while in June significantly fewer taxa were associated with *Lagarosiphon* than in January (Tukey Q test, $p < 0.05$). No significant correlations were found between the number of taxa and any of the physicochemical parameters recorded during the study period (Spearman Rank correlation, $p > 0.05$).

Evenness in macroinvertebrate assemblage was at its lowest August 2008 and highest in June (Figure 4.6b). Evenness generally increased from August 2007 to December, decreased in January and February, rose in June and sharply dropped in July and August 2008 (Figure 4.6b). No significant differences occurred in mean monthly evenness in the period from August 2007 to January (Mann Whitney U tests, $p > 0.05$). Assemblage evenness in June was significantly greater compared to the periods August 2007 to November, and January to August 2008 (Mann Whitney U tests, $p < 0.05$). Evenness in August 2008 was significantly lower than in all other months (Mann Whitney U tests, $p < 0.05$) except January (Mann Whitney U tests, $p > 0.05$).

Table 4.4. Spearman correlation coefficients[a] for the relationship between macroinvertebrates associated with *Lagarosiphon* and water physicochemical variables.

	TP	PO_4^{3-}	TN	NH_4^+	NO_3^-	PH	T (^{O}C)	Conductivity	Turbidity	DO	Dam level
Dugesia	**0.57**	-0.34	0.01	**-0.48**	0.11	0.07	**-0.61**	0.01	-0.01	0.21	0.12
Naididae	0.20	-0.14	-0.04	-0.30	0.05	0.04	**-0.42**	0.06	**-0.34**	0.21	0.09
P. acuta	0.18	0.06	0.26	-0.04	**0.45**	**0.37**	-0.17	-0.17	0.19	**0.44**	**-0.57**
Hydracarina	0.06	-0.10	0.31	-0.23	**0.47**	-0.10	-0.11	0.05	-0.07	**-0.29**	0.07
C. hislopi	**-0.36**	0.14	-0.32	0.25	-0.01	**-0.40**	-0.03	**0.34**	**-0.36**	**-0.58**	**0.75**
Ostracoda	**0.72**	**-0.44**	0.20	-0.35	0.20	**0.32**	**-0.50**	-0.11	0.15	**0.34**	-0.16
Caenis	**0.64**	**-0.36**	-0.07	**-0.61**	-0.05	0.03	**-0.67**	0.19	0.10	0.24	0.08
Cloeon	-0.13	-0.01	0.08	0.29	0.19	0.07	-0.11	0.09	-0.25	-0.21	**0.39**
Pseudagrion	0.07	0.02	-0.21	-0.07	-0.03	-0.09	**-0.42**	0.05	-0.26	-0.03	**0.39**
Enallagma	-0.22	0.01	-0.07	-0.22	-0.01	**-0.32**	0.19	0.16	-0.27	**-0.42**	0.21
Ischnura	-0.32	0.21	-0.30	0.13	-0.02	-0.15	-0.17	0.07	**-0.35**	-0.17	**0.35**
Micronecta	**-0.37**	-0.10	0.33	0.15	0.13	0.14	0.04	-0.11	-0.16	**-0.48**	**0.42**
Orthotrichia	**0.47**	-0.17	0.17	**-0.44**	0.12	**0.44**	-0.14	-0.26	**0.31**	**0.44**	**-0.43**
Ecnomus	0.03	-0.15	0.02	-0.24	**-0.39**	-0.08	**-0.31**	0.04	-0.05	-0.01	0.15
Chironominae	-0.31	0.00	-0.19	0.12	-0.14	0.05	-0.06	-0.12	**-0.31**	**-0.38**	**0.53**
Tanypodinae	-0.01	-0.23	0.00	0.03	-0.05	0.14	-0.26	0.09	**-0.34**	-0.08	**0.37**
Orthocladiinae	**0.55**	-0.27	0.00	**-0.44**	-0.06	-0.03	**-0.64**	0.05	-0.10	0.20	0.11
Total Abundance	**0.44**	**-0.47**	-0.04	**-0.48**	0.12	0.01	**-0.50**	0.09	-0.13	0.08	0.17

[a] Significant correlations ($P < 0.05$) are presented in bold type

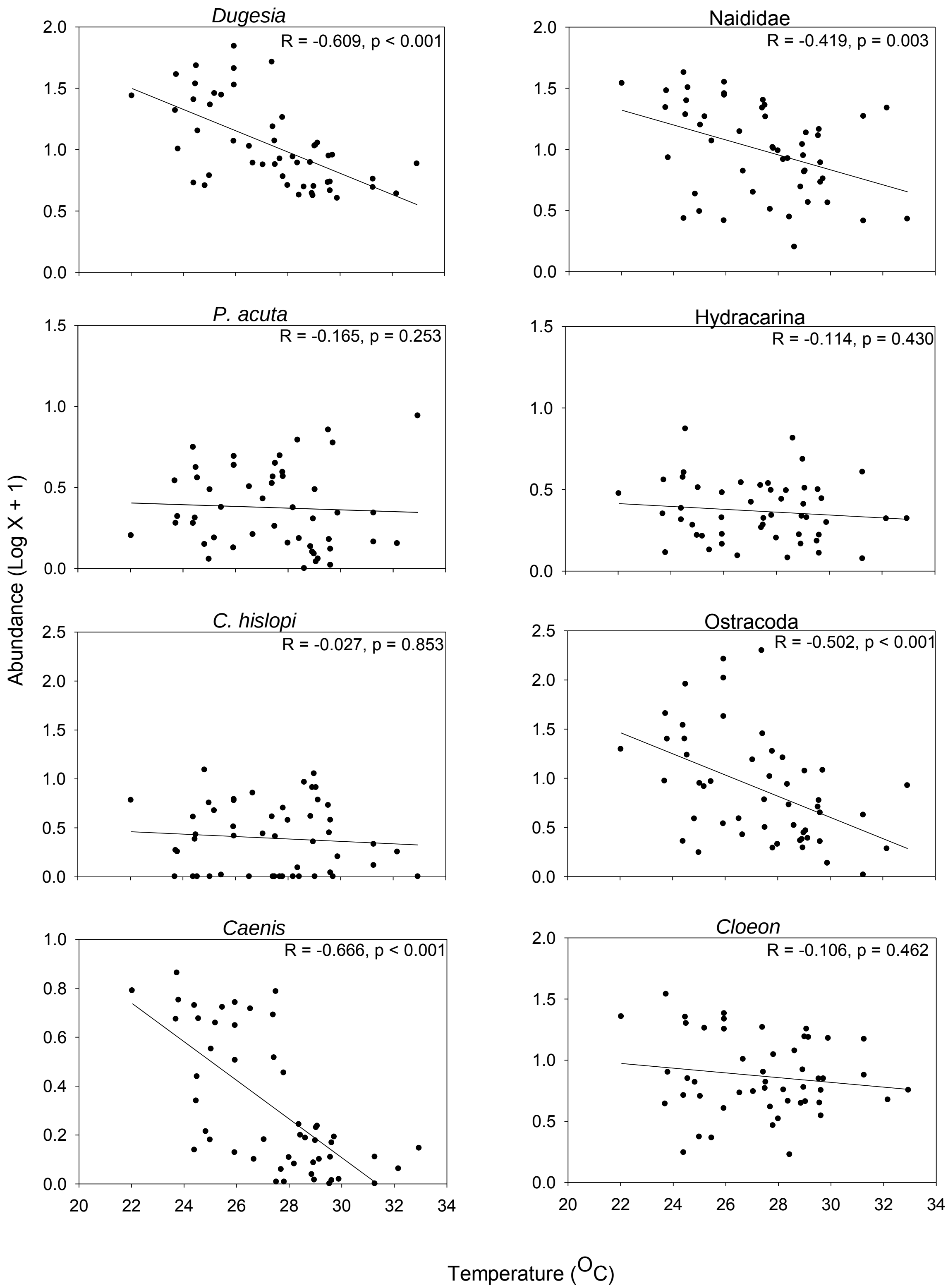

Figure 4.5a. The change in abundances (no. per gram dry mass of *Lagarosiphon*) of the common macroinvertebrate taxa associated with *Lagarosiphon* with change in water temperature. The Spearman r and *p* values are shown for each taxon.

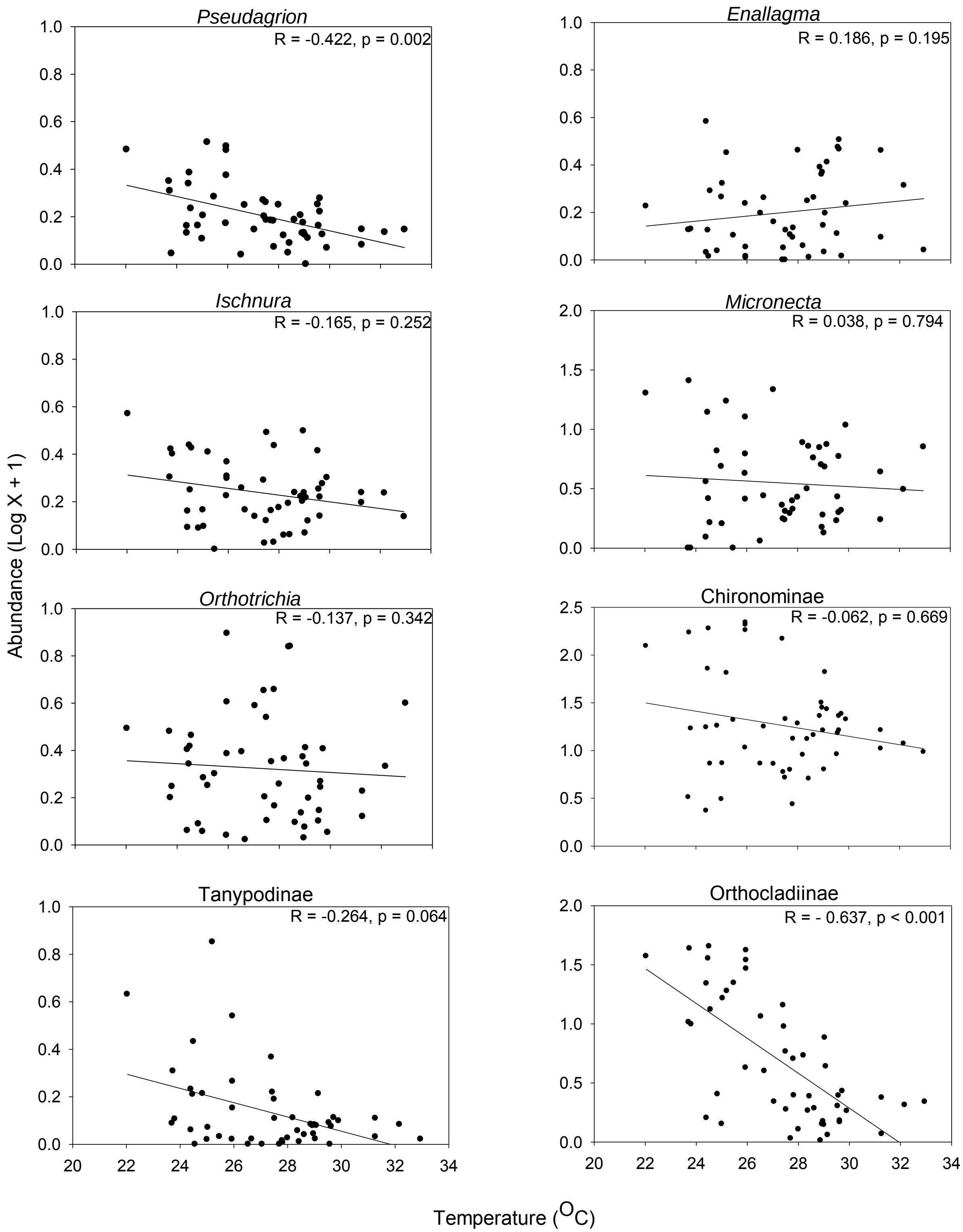

Figure 4.5b. The change in abundances (no. per gram dry mass of *Lagarosiphon*) **of the main macroinvertebrate taxa associated with** *Lagarosiphon* **with change in water temperature. The Spearman r and *p* values are shown for each taxon.**

The lowest average value (1.74 ± 0.09) of *H′*, the Shannon index of diversity, was obtained in August 2008 and the highest (2.49 ± 0.05) in June (Figure 4.6c). Generally, diversity differed significantly among some months (Kruskal-Wallis ANOVA, H = 31.21, DF = 12, p = 0.002). Diversity increased from August 2007 to December, and relatively low values were recorded from January to May, which were followed by an increase in June and sharp decrease in July and August 2008 (Figure 4.6c). Diversity in June was significantly greater than in August 2007 to October, February to March, and July and August 2008, while in September it was significantly greater than in October, February, April, July and August 2008. The mean diversity recorded in August 2008 was significantly less (Mann Whitney tests, $p < 0.05$) compared to all the other months during the study period except February, with which there was no significant difference (Mann Whitney U test, $p > 0.05$). In July diversity was significantly lower than in September, November, December and June (Mann Whitney U tests, $p < 0.05$). Thus macroinvertebrate community evenness and diversity were relatively low in July and August 2008 compared to other months during the study period suggestion numerical dominance of few taxa in the last two months of the study.

Evenness was positively and significantly correlated with total nitrogen concentration (Spearman Rank correlation, R = 0.375, p = 0.037). The Shannon index of diversity was negatively and significantly correlated with ammonium concentration (Spearman Rank correlation, R = -0.418, p = 0.019) but positively and significantly correlated with nitrate concentration (Spearman Rank correlation, R = 0.494, p = 0.005).

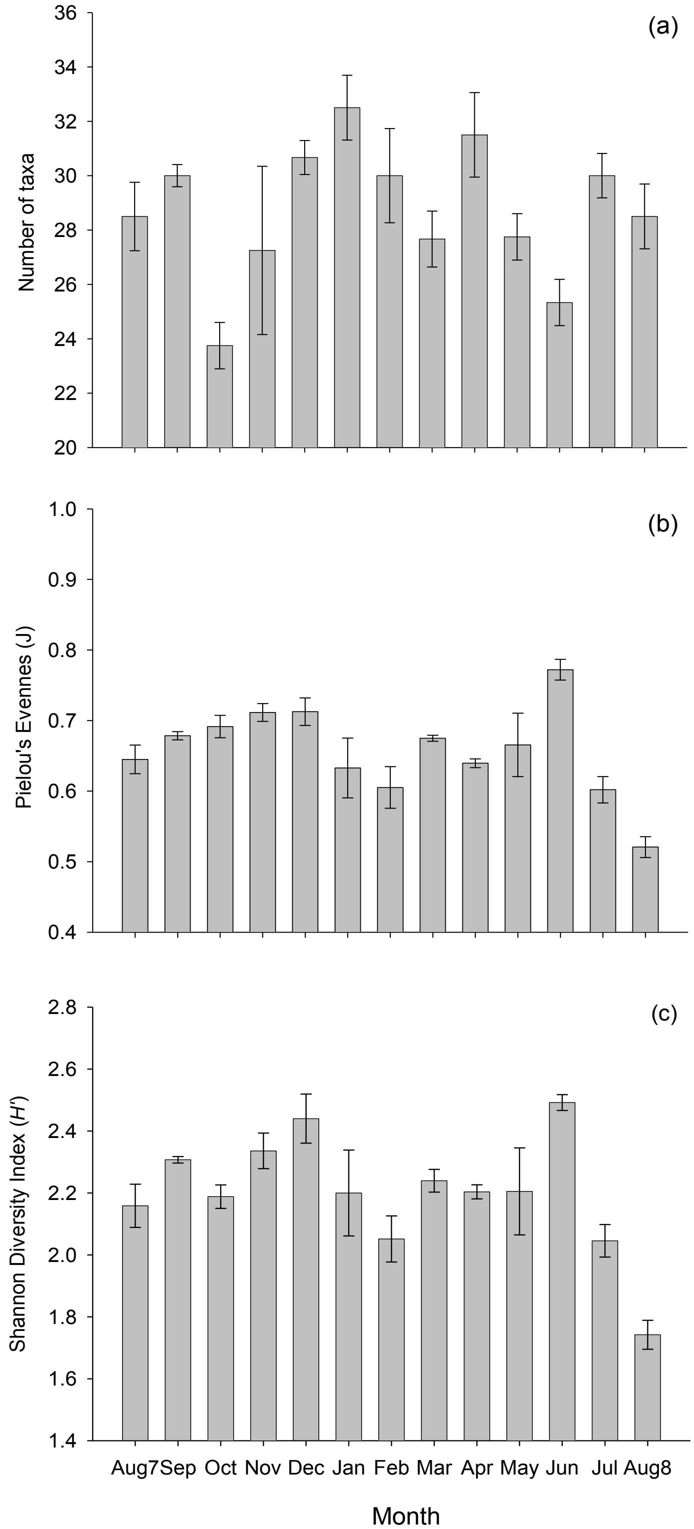

Figure 4.6. Number of taxa, evenness and diversity of epiphytic macroinvertebrates associated with *Lagarosiphon* in Lake Kariba.

4.3.8 Non-parametric multivariate analysis of macroinvertebrate community structure

Analysis of similarities (ANOSIM) was also used to determine whether there were any significant differences in macroinvertebrate community structure associated with *Lagarosiphon* among months. The ANOSIM test showed significant differences between most of the pair-wise comparisons (Table 4.5). The temporal differences in macroinvertebrate community structure are illustrated in the 2-D MDS ordination plot (Figure 4.7) and the Bray-Curtis Similarity cluster analysis plot (Figure 4.8). Figure 4.7 suggests that samples in each month were generally similar and that the macroinvertebrate community could be separated into five major clusters, 1 (August 2007 – September), 2 (October – December), 3 (January – March), 4 (April – June) and 5 (July – August 2008). Cluster analysis also shows that similarity between samples in each month was high and normally greater than 70% and that similarity in macroinvertebrate assemblage between months was generally over 65% (Figure 4.8). Cluster analysis separated samples into the six major groups, 1 (August 2007 – October), 2 (October – December), 3 (January – February), 4 (March – May), 5 (June) and 6 (July – August 2008) (Figure 4.8). The analysis suggests that invertebrate assemblage obtained in June was quite distinct from the other months. The grouping of samples based on invertebrate assemblages was quite similar to that obtained when water samples where clustered based on physicochemical condition (see Figure 4.2).

The SIMPER procedure was carried out on macroinvertebrate data to determine which taxa were the main components enhancing similarity between samples in each month and which were primarily responsible for the dissimilarity between months. A cut-off cumulative percentage of 50% was used to restrict the analysis to the key species. The similarities between samples in the each month are shown in Table 4.6. Generally, the samples collected in each month were similar, with over 70% similarity, and with the lowest similarity of 73.1%, recorded in November. In August 2007, September and October, *Dugesia* sp, Naididae, Orthocladiinae and Ostracoda were largely responsible for the similarity among the samples. *Dugesia* contributed more than 10% to similarity between samples in each month of the study period. In November, Ostracoda, *Micronecta* and Chironominae also accounted for a high proportion of the macroinvertebrate community similarity. The similarity in the December samples was also largely due to *P. acuta*, Ostracoda and Chironominae.

In January, February and March similarity in macroinvertebrate community among samples in each month was largely due to large contributions by *Dugesia*, Naididae, *Cloeon* and Chironominae. Together with *Dugesia*, the concostracan *C. hislopi* made large contributions to the similarities in April, May and June samples. Chironominae in April and May, and Naididae in April and June, as well as, *Cloeon* and *Micronecta* in May and June respectively, also made large contributions to the similarity in samples. In July and August 2008, *Dugesia*, Naididae and Chironominae all made relatively large contributions to sample similarities, as well as Orthocladiinae in July and Ostracoda in August 2008. *Dugesia* contributed relative large proportions to similarities of macroinvertebrate community structure in each of the thirteen months, Naididae and Chironominae in ten and Ostracoda and *Cloeon* in six of the months sampled. Thus the similarity in macroinvertebrate communities in most months was largely due to the dominance of *Dugesia*, Naididae, Ostracoda, Chironominae and *Cloeon*. The ANOSIM and SIMPER results suggest that although there were significant differences in macroinvertebrate assemblage attributable to differences in the abundances of individual taxa, the composition of the macroinvertebrate community was largely similar throughout the study period.

Table 4.5. Results of pairwise tests from 1-way ANOSIM showing R-statistics and P values for each pair of months over a thirteen month period from 2007 to 2008 (R values range from 0 = pair indistinguishable; to 1 = pair strongly differ).

		Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Aug	R	0.111	0.771	0.875	0.963	0.885	1.000	1.000	1.000	1.000	1.000	0.979	1.000
	P	0.371	0.029	0.029	0.029	0.029	0.029	0.029	0.029	0.008	0.029	0.029	0.008
Sep	R		0.500	0.852	1.000	0.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	P		0.057	0.029	0.100	0.029	0.029	0.100	0.029	0.018	0.100	0.029	0.018
Oct	R			0.573	0.889	0.896	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	P			0.029	0.029	0.029	0.029	0.029	0.029	0.008	0.029	0.029	0.008
Nov	R				0.352	0.729	0.875	0.87	0.979	0.969	0.944	0.938	0.994
	P				0.057	0.029	0.029	0.029	0.029	0.008	0.029	0.029	0.008
Dec	R					0.611	0.963	0.889	1.000	1.000	1.000	1.000	1.000
	P					0.029	0.029	0.100	0.029	0.018	0.100	0.029	0.018
Jan	R						0.281	0.574	0.656	0.881	0.926	0.979	0.994
	P						0.114	0.029	0.029	0.008	0.029	0.029	0.008
Feb	R							0.185	0.531	0.906	0.963	1.000	1.000
	P							0.257	0.029	0.008	0.029	0.029	0.008
Mar	R								-0.111	0.692	0.889	1.000	1.000
	P								0.800	0.018	0.100	0.029	0.018
Apr	R									0.250	0.870	1.000	1.000
	P									0.111	0.029	0.029	0.008
May	R										0.949	0.969	1.000
	P										0.018	0.008	0.008
Jun	R											1.000	1.000
	P											0.029	0.018
Jul	R												0.763
	P												0.008

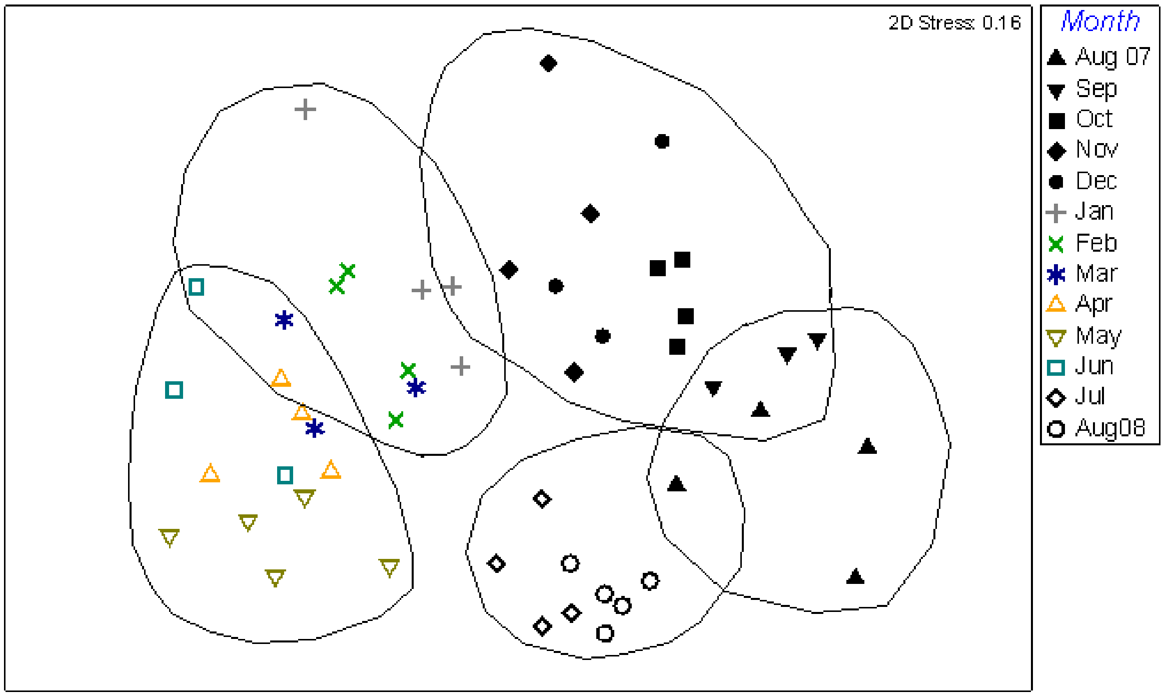

Figure 4.7. MDS 2D ordination on square-root-transformed macroinvertebrate taxa abundance data. The figure shows that samples in each month were generally similar but that temporally, macroinvertebrate community structure was separated into five major groups.

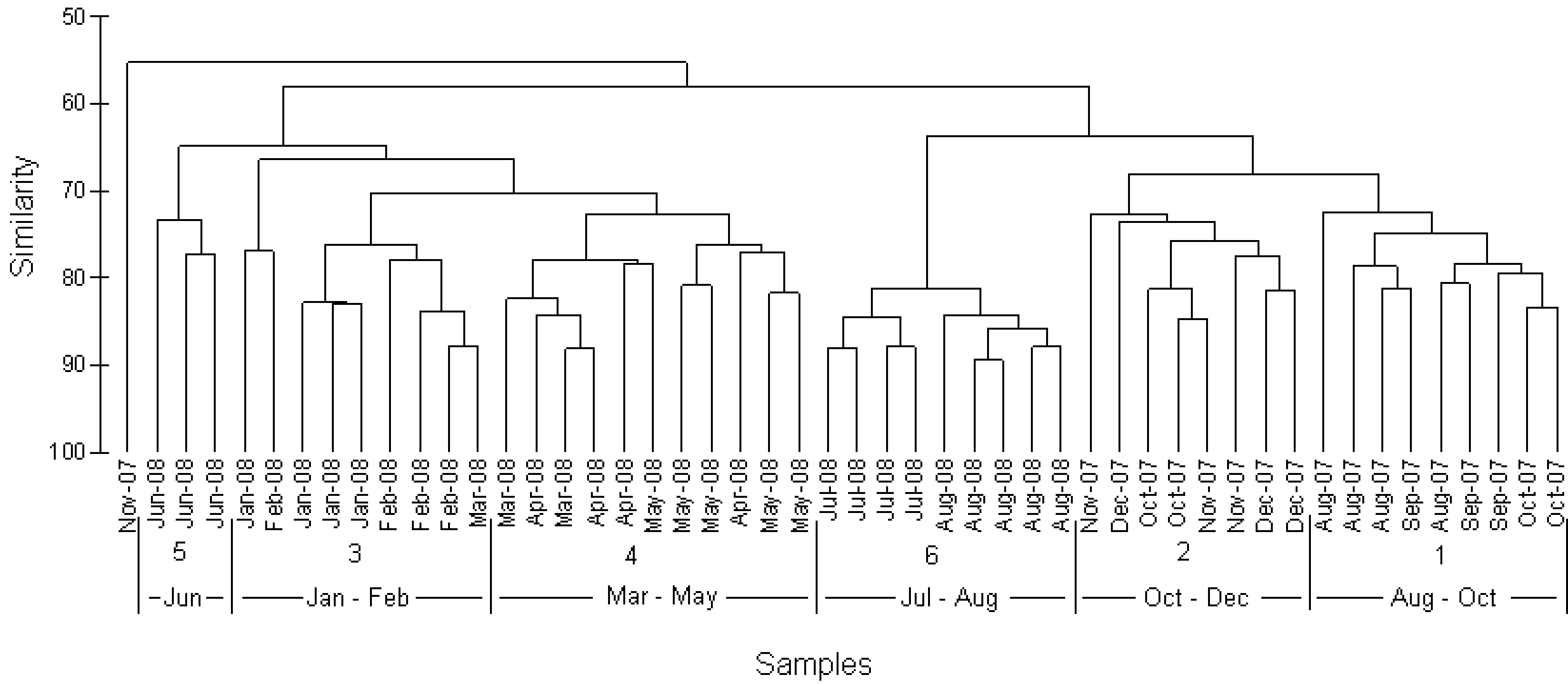

Figure 4.8. Bray-Curtis Similarity cluster analysis plot of the similarity in epiphytic macroinvertebrate assemblage associated with *Lagarosiphon* in Lake Kariba. This figure shows that macroinvertebrate assemblage structure was separated into 6 major clusters over the 13-month study period.

Table 4.6. Results of SIMPER analysis showing the contributing to similarity between samples in each month of the most common macroinvertebrate taxa associated with *Lagarosiphon*. Also shown is the average similarity in macroinvertebrate assemblage of samples obtained in each month.

	Aug-07	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug-08
Dugesia	13.35	14.23	14.88	12.26	12.30	12.15	10.03	11.05	10.16	10.19	15.87	11.20	11.35
Naididae	12.69	14.71	13.43			11.73	13.13	12.60	11.72		8.99	10.01	9.78
P. acuta					9.78								
C. hislopi									9.72	11.18	11.61		
Ostracoda	13.38	8.93	13.34	14.10	13.22								13.09
Cloeon						14.81	12.10	9.25		12.75			
Micronecta				14.20							12.32		
Chironominae				13.08	12.32	17.10	18.97	19.16	18.95	16.33		14.33	15.74
Orthocladiinae	13.10	13.04	10.49									10.84	
Average similarity (%)	75.66	78.88	80.06	73.05	78.58	75.16	77.67	76.82	76.5	76.83	74.63	85.69	85.79

Analysis of the invertebrate assemblages on *Lagarosiphon* using SIMPER for dissimilarities among months showed that Ostracods, Chironominae, Orthocladiinae, Naididae, *Micronecta* and *C. hislopi* were important in distinguishing between 75.6%, 73.1%, 66.7%, 65.4%, 65.4%, and 53.8% of the different monthly pairs respectively. In the paired comparisons in which they made relatively high contributions to the dissimilarity, Ostracods, Chironominae and Orthocladiiane contributed more than 5% to the dissimilarity in 95%, 86% and 88% pairs respectively, and more than 10% dissimilarity in 34%, 28% and 50% pairs respectively. Naididae, *Micronecta* and *C. hislopi* contributed between 5 to 10% dissimilarity to 85%, 69% and 71% respectively, and more than 10% dissimilarity to 4%, 19% and 21% respectively, of the pairs to which they made relatively high contributions to dissimilarities.

The lowest average dissimilarity between any two months was 18.6% between July and August 2008 and the highest, 53.8%, between June and August 2008. Overall, 15.4%, 43.6% and 41.0% pairs had average dissimilarity values of below 30%, greater than 30% but less than 40%, and greater than 40% respectively. Thus there was relatively low dissimilarity in macroinvertebrates associated with *Lagarosiphon* among most months. The differences in the abundance of Naididae, Ostracoda, *C. hislopi*, *Micronecta*, Chironomiane and Orthocladiinae were important in distinguishing macroinvertebrate community structure among the different months.

4.4 Discussion

Although submerged aquatic macrophytes are known to support a variety of animal species and are important in the functioning and productivity of aquatic systems, very few studies have been done on the aquatic vegetation in African freshwater systems, especially with respect to epiphytic invertebrate communities.

This study explored the temporal changes in macroinvertebrate assemblages associated with *Lagarosiphon* in shallow marginal waters of Lake Kariba and their relationships to water physical and chemical properties over a thirteen-month period. Studies on temporal aspects of freshwater macroinvertebrates have been inconclusive, with some showing substantial variation (e.g., Mykrä 2006) while others noted relatively stable persistent invertebrate composition (e.g., Robinson *et al.* 2000). The current study shows that although significant differences occurred in the abundance of individual taxa, the taxonomic composition of the macroinvertebrate assemblage was generally similar throughout the study period. According to Robinson *et al.* (2000) community structure is generally stable where local environmental conditions do not fluctuate substantially over time.

4.4.1 Invertebrates associated with *Lagarosiphon* in shallow waters of Lake Kariba

Sixteen macroinvertebrate taxa commonly occurred on *Lagarosiphon*. The numerically dominant taxon was the chironomid subfamily Chironomidae which made up 31.5% of the total number of organisms collected during the study. Other taxa that contributed more than 10% to the overall total were *Dugesia* (11.7%), Naididae (10.3%) and Ostracoda (15.6%).

Oligochaetes and chironomids have a cosmopolitan distribution. They both have species that occur in virtually all types of water. Oligochaetes and chironomids are usually among the most abundant taxa in epiphytic macroinvertebrate assemblages in freshwater environments (e.g., Balci 2002, Balcombe *et al.* 2007, Bogut *et al.* 2007). Naidid oligochaetes can exploit a great variety of habitats, including: sediments (Wetzel & Taylor 2001), macrophytes (Alves & Gorni 2007), bryophytes (Gorni & Alves 2007) and sponges (Corbi *et al.* 2005, Gorni & Alves 2008). Gorni & Alves (2008) showed that in two reservoirs in Brazil many naidid species are generally associated with aquatic macrophytes, with greater abundances occurring on morphologically complex macrophyte species. The tolerance of Chironomidae to a wide range of environmental conditions compared to other groups of aquatic insects is largely because of their broad range of morphological, physiological and behavioural adaptations (Merritt & Cummins 1996). This enables them to dominate macroinvertebrate assemblages in freshwater systems. Submerged macrophytes also tend to trap detritus and organic matter, which promotes the establishment of relatively large numbers of detritivorous taxa such as the oligochaetes and collector-gathers such as the Ostracoda (Albertoni *et al.* 2007). Within a given trophic level, abundant species normally tend to receive the greatest attention from predators (Montoya *et al.* 2006). Thus chironomids are probably the most important food items for fish that use *Lagarosiphon* beds for cover from predators and as a source of food in Lake Kariba.

Freshwater Turbellaria worms are widely distributed and generally inhabit non polluted water bodies (Malhão *et al.* 2007). Due to their photonegative sensitivity, members of the Dugesiidae family occur mainly in shallow sheltered waters of lakes (Reynoldson & Young 2000). Ostracods are also common in most freshwater bodies and occur as benthic or periphytic animal communities (Martens *et al*. 2008).

Earlier work on Lake Kariba showed the dominance of Chironomidae in mud (McLachlan 1968, Bowmaker 1973), macrophytes (McLachlan 1969a, Bowmaker 1973) and submerged trees (McLachlan 1970b). Bowmaker (1973) also showed the numerical dominance of chironomids on three submerged macrophytes, *Ceratophyllum* (45.9% of total number of organisms), *Potamogeton* (70.1%) and *Lagarosiphon* (37.9%). The early work by McLachlan in the late 1960s, which largely focused on mud and submerged trees, recorded a comparatively small number of macroinvertebrate species, a total of only 25 species, comprising 15 species of Chironomidae, 4 of Trichoptera, 3 of Oligochaeta, 2 of Ephemeroptera and 1 of Gastropoda. Bowmaker (1973) recorded a total 26 species from *Ceratophyllum*, *Potamogeton* and *Lagarosiphon*, and 98 species from the floating macrophyte *Salvinia molesta*. In the present study 86 macroinvertebrate taxa were recorded on *Lagarosiphon*, which is in sharp contrast to the earlier studies, which found that submerged macrophytes were associated with comparatively low numbers of macroinvertebrate taxa. The relatively low numbers of taxa recorded during the early years of Lake Kariba were probably due to heavy surface coverage by *Salvinia*, which inhibited widespread occurrence of submerged macrophytes (Mitchell 1969) and made physicochemical conditions in the littoral zone unfavourable for the development of many invertebrate organisms (McLachlan 1969a). Thus it seems as if the virtual disappearance of *Salvinia* has resulted in an increase in the macroinvertebrate taxa associated with *Lagarosiphon*, which is now the most widespread and abundant aquatic macrophyte in the lake.

4.4.2 Temporal aspects in physicochemical conditions

During the sampling period of the current study there were distinct temporal/seasonal changes in physicochemical conditions especially with respect to water temperature and water levels. Generally water temperatures rose from August 2007 to January 2008, and then gradually decreased thereafter, while water level decreased from August 2007 to January 2008 and increased thereafter (see Figure 4.1). These were probably the two most important water physicochemical variables in the lake. Although significant differences were observed, there were no distinct temporal patterns in pH, conductivity, turbidity, dissolved oxygen concentration and nutrient concentrations.

4.4.3 Effect of water physiochemical characteristics on invertebrates associated with *Lagarosiphon*

The temporal and spatial abundance of macroinvertebrates associated with vegetation in lentic systems is influenced by a range of environmental characteristics, including water chemistry, habitat complexity, and hydrology (Balcombe *et al.* 2007). Water chemistry affects epiphytic macroinvertebrates through the direct physiological effects of variables such as temperature (Sweeney & Vannote 1986, Hawkins *et al.* 1997) and pH (France 1990). Water temperature also has indirect effects on epiphytic algal production (Kornijow 1989, Pieczyńska *et al.* 1999) an important food base for some macroinvertebrate taxa (Merritt & Cummings 1996) through its effect on nutrient cycling. In tropical and subtropical systems continuously warm temperature allow for high rates of microbial activity, which generally accelerates nutrient cycling and results in high primary production (Squires *et al.* 2009). Comparatively, in cold artic water bodies the rates of nutrient recycling by microbial organisms are generally low (Rouse 1997), which results in low primarily productivity and low available food resources for invertebrates.

Temperature is one of the most important abiotic factors in the life of ectotherms as it affects every characteristic of their physiology (Pörtner *et al.* 2006). All biochemical and biological processes of aquatic invertebrates such as growth, development, population cycles, biomass turnover times and trophic interactions have rates of operation that are temperature dependent (Ward 1992, Wotton 1995, Lessard & Hayes 2003).

The abundances of most of the major taxa associated with *Lagarosiphon* showed significant temporal differences. This study suggests that temperature and water level were the main factors affecting invertebrate abundances on *Lagarosiphon*. Abundances of *Dugesia*, Naididae, Ostracoda, *Caenis*, *Orthotrichia* and Orthocladiinae showed distinctive temporal variation, generally characterised by gradual decrease from August 2007 to December, relatively low numbers between December and June, and increase in July and August 2008. The abundances *Dugesia*, Oligochaeta, Ostracoda, *Caenis, Pseudagrion*, *Ecnomus* and Orthocladiinae were significantly and inversely correlated with water temperature. Although there were significant differences among some of the months, the abundance of *Cloeon* did not show a clear or distinct temporal pattern. The only taxon whose abundance did not change significantly during the study period was Hydracarina.

4.4.3.1 Effects of water temperature on invertebrates

In temperate freshwater ecosystems, although increase in temperature generally alters the composition of aquatic communities (Carpenter *et al.* 1992), the production and abundance of fish (Shuter & Post 1990) and invertebrates (Hogg & Williams 1996) may be enhanced. In the current study I originally expected that individual taxa as well as overall macroinvertebrate abundance would increase with increasing temperature. The abundances of seven of the common and frequent macroinvertebrate taxa (*Dugesia*, Oligochaeta, Ostracoda, *Caenis*, *Pseudagrion*, *Ecnomus* and Orthocladiinae), and the total abundance of macroinvertebrates, decreased at relatively high water temperatures. A number of studies have shown a decrease in macroinvertebrate abundance and diversity following an average temperature increase of about 7^{O}C (e.g., Wellborn & Robinson 1996, Hogg *et al*. 1995). The water temperature recorded in the shallow marginal waters of the lake during the study period ranged from 22^{O}C to 33^{O}C, a difference of more than 10^{O}C. Generally, an increase in water temperature of about 10^{O}C leads to a doubling of the metabolic rate of organisms, which combined with reduced oxygen supply, results in enhanced stress to the organisms (Dallas 2008).

Ectotherms have developed different ranges of thermal tolerance, which may limit their distribution (Pörtner 2001). Generally, early life history stages such as eggs and larvae tend to have narrower thermal tolerance ranges and lesser tolerances to adverse temperature conditions in comparison to adult stages (Anger 2001, Thatje 2005). The present study suggests that water temperatures above 28^{O}C had adverse effects on a number of macroinvertebrates taxa associated with *Lagarosiphon*, which resulted in reduced individual taxa and overall macroinvertebrate abundance. At water temperatures greater than 28^{O}C the abundances of *Dugesia*, Naididae, Ostracoda, *Caenis*, *Pseudagrion*, Tanypodinae and Orthocladiinae were greatly reduced. In studies done in Australian, European and North American water bodies (e.g., Chandler 1966, Lock & Reynoldson 1976, Hay & Ball 1979, Armitage & Young 1990, Roca *et al.* 1992) water temperature has been shown to be the major factor affecting the distribution and abundance of planarians. In laboratory studies Claussen *et al.* (2003) found that *Dugesia dorotecephala*, which is one of the most widely distributed and eurythermal triclads in North America generally selected temperatures between 12^{O}C and 28^{O}C. They also found that although *D. dorotecephala* could survive temperatures of about 33 ^{O}C for nearly 12 hours, its incipient lethal temperature were around 30.5^{O}C. Pattée *et al.* (1973) found that for another cosmopolitan triclad, *D. tigrina*, the upper incipient lethal temperature to be about 29^{O}C.

In New Zealand, naidids have been found in geothermal systems where they are able to tolerate temperature up to 34^{O}C (Winterbourn (1968) quoted in Boothroyd (2009). Contrary, Duggan *et al.* (2007) who also studied stream macroinvertebrates in geothermal areas in New Zealand, found that the Oligochaeta were strongly associated with cooler areas. In tidal creeks of the south eastern United States, Gillett *et al*. (2007) found that the naid *Paranais litoralis*, which was the only non-tubificid oligochaete obtained in large numbers, was present during months when mean daily temperature was less than 20^{O}C (November to March) and absent during the other months of the year when mean daily temperature were generally greater than 30^{O}C.

There are about 189 aquatic genera and 1,936 subjective aquatic species of extant non-marine Ostracoda species, with the Cyprididae family making up about half of both species and genera diversity (Martens *et al*. 2008). According Martens *et al.* (2008) the order is characterised by endemicity and only about 10% of all species have intercontinental distribution. Out of ten cosmopolitan ostracod species, Külköylüoglu (2000) (quoted in Külköylüoglu 2004) found that 6 had upper temperature tolerance limits equal or less than 30^{O}C, 2 of between 31^{O}C–35^{O}C, 1 of between 36^{O}C–40^{O}C and 1 an upper tolerance range greater than 40^{O}C. Thus it seems that most ostracod species with a worldwide distribution and that are found in virtually all kinds of water have upper temperature tolerances that are below 30^{O}C. This seems to be the case with ostracods associated with *Lagarosiphon* in Lake Kariba.

Water temperature is one of the most important factors that influences the occurrence and distribution of Ephemeropteran larvae (Wellborn & Robinson 1996) and high water temperatures have been shown to adversely affect mayfly larval recruitment and growth (Sweeney 1993). Pritchard *et al*. (1996) analysed egg hatching in 21 species of Ephemeroptera and found that most were adapted to warm water temperatures. According to Sweeney & Vannote (1978) and Provonsha (1990) egg production for many *Caenis* species is adversely affected if during larval growth water temperatures are warmer or cooler than optimal conditions. During the current study high temperatures were associated with very low numbers of *Caenis*. The current study also showed that although *Cloeon*, the most abundant ephemeropteran genera, was not significantly affected by variation in temperature, the total number of ephemeropterans was significantly reduced at high temperatures. Thus water temperatures greater than 28^{O}C in inshore waters of Lake Kariba are probably not optimal for growth, development and reproduction of ephemeropterans.

Temperature has been shown to affect physiology of odonates including development rate, phenology, seasonal regulation, immune function and the production of pigment for thermoregulation (Hassal & Thompson 2008). Three coenagrionid taxa, *Pseudagrion*, *Enallagma* and *Ischnura*, were collected from *Lagarosiphon* during this study and the abundance of *Pseudagrion* was significantly lower at high temperatures. They are nearly 100 species of *Pseudagrion* that have been recorded in Africa, and the genera is known to occupy all freshwater habitats in tropical Africa and Madagascar, dominating from pools in the Kalahari to alpine streams on the Kilimanjaro (Dijkstra 2007). The current study suggests that for some species of *Pseudagrion* water temperatures greater than 28^{O}C may not be optimal for growth and development.

High water temperatures have been shown to adversely affect larval recruitment and growth some chironomid species (e.g., Flory & Milner 2000). Coffman (1989) suggested that tropical chironomid communities are less regulated by temperature than those in temperate streams. In the current study I found that the overall abundance of dipteran taxa on *Lagarosiphon* was considerably reduced at high water temperatures. Of the three main chironomid subfamilies Chironominae, Tanypodinae and Orthocladiinae associated with *Lagarosiphon*, the abundances of the later two subfamilies were markedly reduced at high temperatures, while the abundance of Chironominae was not significantly affected by variation in water temperature. High water temperatures have been associated with lowered abundances of chironomids in a number of water bodies (e.g., Hogg & Williams 1996, Tixier *et al.* 2009). Studies in temperate regions have also shown that Chironominae generally tend to be more abundant in warm waters while Orthocladiinae dominate in cold habitats (e.g., Rossaro 1991, Walker & MacDonald 1995).

Thus, variation in water temperature had a significant effect on invertebrate assemblage associated with *Lagarosiphon*. Although in might be suggested that the significantly low numbers of ephemeropteran and chironomids at high temperature were due to emergence, it is worth noting that the abundance of non-emerging taxa (*Dugesia*, Naididae and Ostracoda) also decreased significantly at high temperatures.

The effect of temperature on the invertebrate assemblage in shallow inshore waters of Lake Kariba needs further investigation. Investigations on thermal tolerances, especially the effect of temperature between the upper 20^{O}Cs and lower 30^{O}Cs, on invertebrate growth and reproduction may enhance our knowledge of the dynamics of invertebrate assemblages.

4.4.3.2 Effects water level on invertebrates

Of the nine taxa that were significantly affected by variation in water levels, seven (*C. hislopi*, *Cloeon*, *Pseudagrion*, *Ischnura*, *Micronecta*, Chironominae and Tanypodinae) increased in abundance at high water levels, while two (*P. acuta* and *Orthotrichia*) decreased. Overall though, water levels had no significant impact on total invertebrate numbers associated with *Lagarosiphon*.

The increase in water levels, especially between April and June, during which levels rose quite rapidly, was not followed by an immediate increase in macroinvertebrate abundance, probably due to the relatively low temperatures at the time. Increase in water level avails nutrients from newly flooded areas, which increases primary production and thus increasing availability of food items for grazing invertebrates. But relatively low temperatures from April to June probably affected biochemical process, reducing primary production and development of macroinvertebrates. A sharp increase in the abundance of all the main macroinvertebrate taxa occurred in July/August probably since water temperatures were beginning to rise and water chemistry conditions within shallow waters where then conducive for rapid macroinvertebrate production. Studies in other water bodies have shown that water level fluctuation is one of the main factors that affects the composition and abundance of macroinvertebrates. Bogut *et al.* (2007) showed that water level fluctuation in a channel in Croatia affected macroinvertebrates associated with four macrophyte species of different morphology, *Nymphoides peltata*, *Ceratophyllum demersum*, *Polygonum amphibium* and *Carex* sp. Balcombe *et al.* (2007) found that invertebrate production associated with emergent macrophytes in a floodplain lake in Australia was largely influenced by water level fluctuation and suggested that the pattern is likely to be common in floodplain water bodies. Higuti & Takeda (2002) also found that water fluctuation in a South American river floodplain influenced chironomid larvae composition and abundance.

4.4.3.3 Effects of other water physicochemical variables

The period of high water temperature and low water levels was characterised by relatively high ammonium concentration and pH, and low total phosphorus concentration and conductivity. The concentration of ammonium was negatively associated with *Dugesia*, *Caenis*, *Orthotrichia*, Orthocladiinae and total invertebrate abundance. Ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) ions are the common ionic forms of inorganic nitrogen in aquatic environments. Under conditions of reduced oxygen levels, high pH and high temperatures, ammonium as well as nitrate may be converted to ammonia, the un-ionised form of ammonium and to nitrite, both of which are toxic to invertebrates and fish (Alonso & Camargo 2003). Thus during periods of high temperatures and low lake water levels, conditions in inshore water of Lake Kariba may have led increased levels of ammonia, and so made conditions suboptimal for the growth and reproduction of some of the invertebrates.

The abundances of five taxa, Hydracarina, *C. hislopi*, *Enallagma*, *Micronecta* and Chironominae were significantly reduced at high dissolved oxygen concentrations. Migration into oxygen depleted zone for refuge from fish predation is a strategy that has been observed in some invertebrates e.g. cyclopoid copepods (Alekseev *et al.* 2006). The significant increase in numbers at low oxygen concentration of some invertebrates on *Lagarosiphon* was therefore probably because of reduction in fish predation at those conditions.

The abundances of *Dugesia*, Ostracoda, *Caenis*, *Orthotrichia* and Orthocladiinae, as well as the total macroinvertebrate abundance were positively associated with the concentration of TP. TP is usually a limiting factor in freshwater ecosystems (Brooks *et al*. 2001) and algal biomass in lakes and reservoirs have been found to be strongly dependent upon TP levels (Guildford & Hecky 2000). According to Magadza (1992)

Lake Kariba is phosphorus limited. Bourassa & Morin (1995) working in streams found significant correlations between invertebrate abundance and TP, as well as between periphyton and TP. They concluded that TP was limiting both primary and secondary productivity in the streams. The results of this study suggest that nutrient dynamics especially, variation in TP levels may be important in structuring macroinvertebrate assemblages associated with *Lagarosiphon* probably, through their effect on algal/periphyton biomass.

4.4.3.4 Conclusions and Recommendations

The findings of this study suggest that temporal variations in temperature plays a key role in structuring the macroinvertebrate assemblage associated with *Lagarosiphon* in the shallow marginal waters of Lake Kariba. It also suggests that fluctuating water levels have a major impact on epiphytic macroinvertebrates. The presence of most of the main taxa throughout the thirteen-month sampling period suggests year-round reproduction, with reduced growth, reproduction and abundances during periods of relatively high water temperatures and low water levels. The results have important implications especially in view of impacts of the predicted increase in mean global temperature due to global climate change (Houghton *et al*. 1996). Increases in water temperatures as a result of climate change have the potential to affect the reproductive success of aquatic invertebrates by altering their phenology, size, and fecundity (Harper & Peckarsky 2006). Increasing temperatures will influence abundance and distribution of species in numerous ways and in Northern Europe changes in trends in average temperature have already had strong impacts on species composition in lakes (Burgmer *et al.* 2007). Mckee & Atkinson (2000) suggest that many aquatic ecosystems will become warmer, and organisms found in habitats with limited capacity to buffer physical change, such as aquatic insects in shallow waters of freshwater systems, will be particularly vulnerable to the warming effect. Schindler (1997) notes that although the temperature changes associated with climate change are relatively small, they may have major impacts for some aquatic species.

Global warming will generally worsen the highly variable and unpredictable climate in Africa, resulting in an increase in extreme events such as droughts and floods (Mason & Joubert 1997). Warming will be greatest over the interior of southern Africa and in the Mediterranean countries of north-west Africa (Hulme *et al.* 2001). Most climate change simulations predict reduced precipitation in southern Africa (Arnell 2004, Bates *et al*. 2008), which will result in reduced runoff, and among the large rivers of the continent the Zambezi River is projected to have greatly reduced flows (Bates *et al.* 2008). This will affect the hydrology of Lake Kariba, affecting the frequency and magnitude of lake level fluctuations. Thus the frequency and duration of the periods of high temperature and low water level in Lake Kariba, which the current study suggests are associated with low macroinvertebrate abundances on *Lagarosiphon* will probably increase. This will probably lead to reduced abundances of macroinvertebrates associated with *Lagarosiphon* and so affecting the food source of fish species. Thus inshore fisheries productivity may adversely be affected in the lake.

This study did not assess the relationship between the macroinvertebrate assemblages associated with *Lagarosiphon* and epiphytic algal production and other biotic factors such as competition and fish predation, all of which are known to influence macroinvertebrate abundance and distribution. The significant and positive association that was noted between most of the major taxa suggest that increase in the abundance of lower trophic levels for example primary consumers such as grazers and collector-gatherers generally result in an increase in the abundances of animals at the higher trophic levels.

Lagarosiphon is the most abundant submersed macrophyte in Lake Kariba (Machena & Kautsky 1988) and this makes it highly important in trophic dynamics of the littoral zone in the lake. This study shows that seasonal variation in temperature and water level is important in structuring the epiphytic macroinvertebrate assemblage, especially the abundances of the major taxa. The results suggest that for a number of invertebrate taxa sub-lethal water temperatures may persist in shallow inshore waters during the hot season. An understanding of invertebrates associated with the macrophyte is essential for the determination of the productivity of the lake. The thermal tolerance ranges of aquatic invertebrates in the southern African region are still to be determined. The current study suggests that water temperatures greater than 28^{O}C in shallow waters of Lake Kariba may not be optimal for a number of invertebrate taxa. Further studies on thermal tolerances of organisms and those that include a greater range of biotic and abiotic factors are needed to enhance knowledge of the ecological factors that structure invertebrate and vertebrate communities in inshore waters of Lake Kariba. In the next chapter I describe some life-history characteristics of the common insect taxa associated with *Lagarosiphon* and their temporal biomass distribution.

CHAPTER 5

BODY SIZE DISTRIBUTION, BIOMASS ESTIMATES AND LIFE HISTORIES OF COMMON INSECT TAXA ASSOCIATED WITH *Lagarosiphon*

5.1 Introduction

Body size is one of the most essential parameters determining the ecological and physiological features of organisms (Peters 1983). A number of generalizations have been made about the relationships between body size and most aspects of life history, population ecology and ecological processes (Blueweiss *et al.* 1978, Peters 1983, Schmid *et al.* 2000). Body size affects fecundity (Savage *et al.* 2004), metabolic rates (Gillooly *et al.* 2001, 2002, Savage *et al.* 2004) population growth rates and density (Savage *et al.* 2004), predator-prey interactions (Tolonen *et al.* 2003, Kuczyńska-Kippen 2005), species abundance (Jonsson *et al.* 2005), dispersal (Kovats *et al*. 1996), and resource use partitioning and food web dynamics (Jonsson *et al.* 2005, Woodward *et al*. 2005). Insect body size has also been used as an important indicator of sub-lethal levels of stress (Alexander *et al.* 2007, 2008). Thus the study of body sizes spectrum of a community can provide useful information on ecological properties and processes in an ecosystem.

Biomass is also an important parameter in the of study community structure, distribution of resources, species, matter, and energy fluxes (Blackburn *et al.* 1993). In both terrestrial and aquatic systems, insects constitute a major portion of the biomass (Gullan & Cranston 1994), and so play pivotal roles in energy transfer processes (Polis & Hurd 1995). In aquatic systems insects and other invertebrates are a major link in the transfer of energy between primary producers and fish. Thus models of the relationship between macroinvertebrate biomass and fish standing stocks and yield (e.g., Matuszek 1978, Hanson & Leggett 1982) and between macroinvertebrate biomass and variables associated with water column productivity or trophic status (e.g., Hanson & Peters 1984) have been established for some lakes.

The submerged macrophyte *Lagarosiphon ilicifolius* is the dominant aquatic plant species in Lake Kariba and therefore plays an important role in the ecology of the lake. The insect and non insect macroinvertebrate taxa contribute about 55.8% and 44.2% respectively of the overall total number of organisms associated with *Lagarosiphon* (Chapter 4). Among the insect taxa the most abundant and common are *Caenis* sp, *Cloeon* sp, Coenagrionidae (*Pseudagrion* sp, *Enallagma* sp and *Ischnura* sp), *Micronecta* sp, and the chironomid subfamilies Chironominae and Orthocladiinae (Chapter 4). Although the insects play an important role in the ecological processes of Lake Kariba very little is known of their life cycles, biomass distributions and productivity in the lake.

The life history information of aquatic invertebrates has been used for a variety of purposes in the study and management of aquatic ecosystems. These include the determination of secondary production (Huryn & Wallace 2000), assessment of environmental impacts and ecological studies on predator-prey dynamics (Wieters *et al*. 2008). Of late freshwater aquatic insects have been used in modelling the effects of global climate change (e.g., Elliot 1996, Bradley & Ormerod 2001, Briers *et al.* 2004). The growth of the nymphal stages of insects is influenced by food quantity and quality as well as by variation in water temperature (Sweeney & Vannote 1986, Elliott 1987). In temperate regions the effect of temperature on the growth and phenology of freshwater insects has been successfully used to model the climatic variability caused by the North Atlantic Oscillation (Elliott 1987, Briers *et al.* 2004).

In this study the temporal changes in size structure and biomass of, *Cloeon* sp, *Caenis* sp Coenagrionidae, *Micronecta* sp, Chironominae and Orthocladiinae associated with *Lagarosiphon* were examined over a thirteen-month study period. The purpose was to explore the seasonal aspects of the life cycle and biomass of the insects and determine the relationship between insect biomass and changes in water physical and chemical properties.

5.2 Materials and Methods

This study was carried over a thirteen-month period, August 2007 to August 2008. Epiphytic invertebrate and water samples were collected on a near weekly basis and 50 invertebrate samples were collected. The total body length (excluding antennae and cerci) of *Caenis* sp, *Cloeon* sp, Coenagrionidae, *Micronecta* sp and the head width of Chironominae and Orthocladiinae were measured using a dissecting microscope fitted with a calibrated graticule. A complete description of the materials and methods is given section 2.3.3

5.3 Results

Monthly size-frequency histograms for the six insect taxa are shown in Figures 5.1 – 5.6. Figure 5.7 shows average biomasses of each taxon for each month of the study period. Almost all the size classes of *Cloeon* (Figure 5.2), Coenagrionidae (Figure 5.3), *Micronecta* (Figure 5.4), Chironominae (Figure 5.5) and Orthocladiinae (Figure 5.6) were present throughout the study period and no distinct cohort patterns were apparent.

The body-size frequency distribution of *Caenis* suggests a univoltine life cycle that is largely completed within a period of six months from July to December (Figure 5.1). *Cloeon* seems to have a multivoltine life cycle, with emergence, mating and ovipositing of eggs mainly occurring in October and February (Figure 5.2). Coenagrionidae, *Micronecta*, Chironominae and Orthocladiinae also appear to be multivoltine with asynchronous hatching and development, although based on the frequency distributions it was not possible to determine the number of generations and the larval development time.

5.3.1 *Caenis* sp.

Between December and March low numbers of *Caenis* occurred on *Lagarosiphon*, but appreciable numbers were obtained between August 2007 and November, and between April and August 2008 (Chapter 4, Figure 4.3b). The proportion of *Caenis* size classes in June was significantly different and dominated by small size classes compared to those in August 2008 (Kolmogorov-Smirnov test, $p < 0.05$). Among the other months there were no significant differences in the size class spectrum (Kolmogorov-Smirnov test, $p > 0.05$). Average body size generally increased from August 2007 to November, and decreased in December (Figure 5.7). The largest number of large-bodied individuals with well developed wing pads was collected from September to November. Between November and June, *Caenis* abundance was drastically reduced (Chapter 4, Figure 4.3b). The data suggest that emergence, mating and ovipositing occur in October/November. The eggs laid undergo diapause between December and March, with relatively small numbers of the eggs hatching as was reflected by the low abundance of nymphs during this period (Chapter 4, Figure 4.3b). The majority of the eggs hatch in July as was shown by increased abundances (Chapter 4, Figure 4.3b) of small-bodied nymphs (Figure 5.7). This suggests a largely univoltine life cycle for *Caenis*, with most eggs hatching in July, rapid growth between July and October, and emergence, mating and ovipositing of eggs in October/November.

Total *Caenis* biomass (Figure 5.8) differed significantly among months (ANOVA, $F_{10, 32} = 16.91$, $P < 0.001$). The mean biomasses in August (2007), September, October and August (2008) were significantly greater than those in the period November to July (Tukey Q tests, $P < 0.05$). The data suggests that *Caenis* reproduction and growth largely occurs in a four month period from July to October.

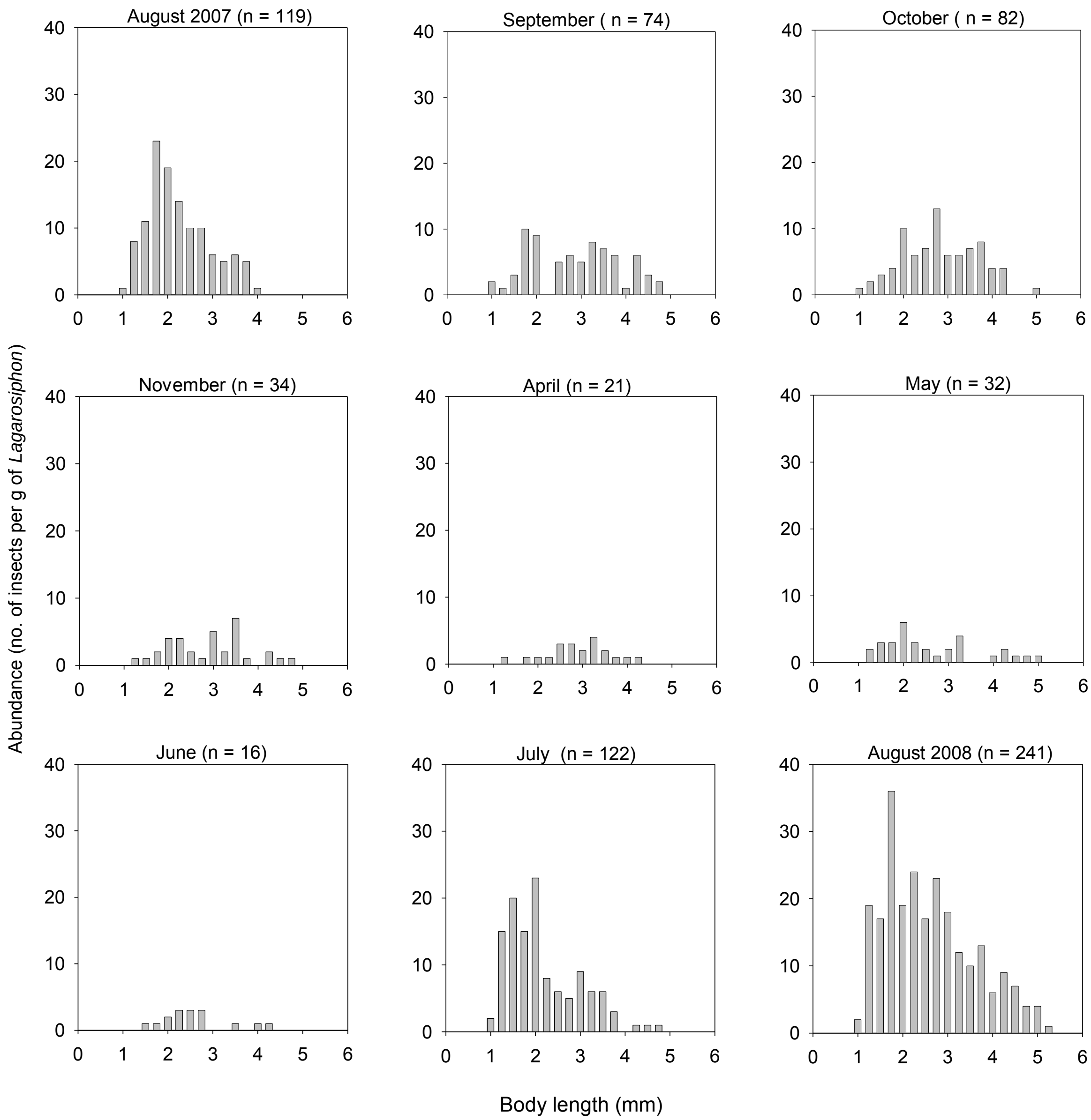

Figure 5.1. Body length distributions of *Caenis* sp. **associated with** *Lagarosiphon* **in Lake Kariba from August 2007 to August 2008. The number of individuals (n) measured are shown for each month. The period from December to March is not shown because** *Caenis* **was largely absent from** *Lagarosiphon* **at that time.**

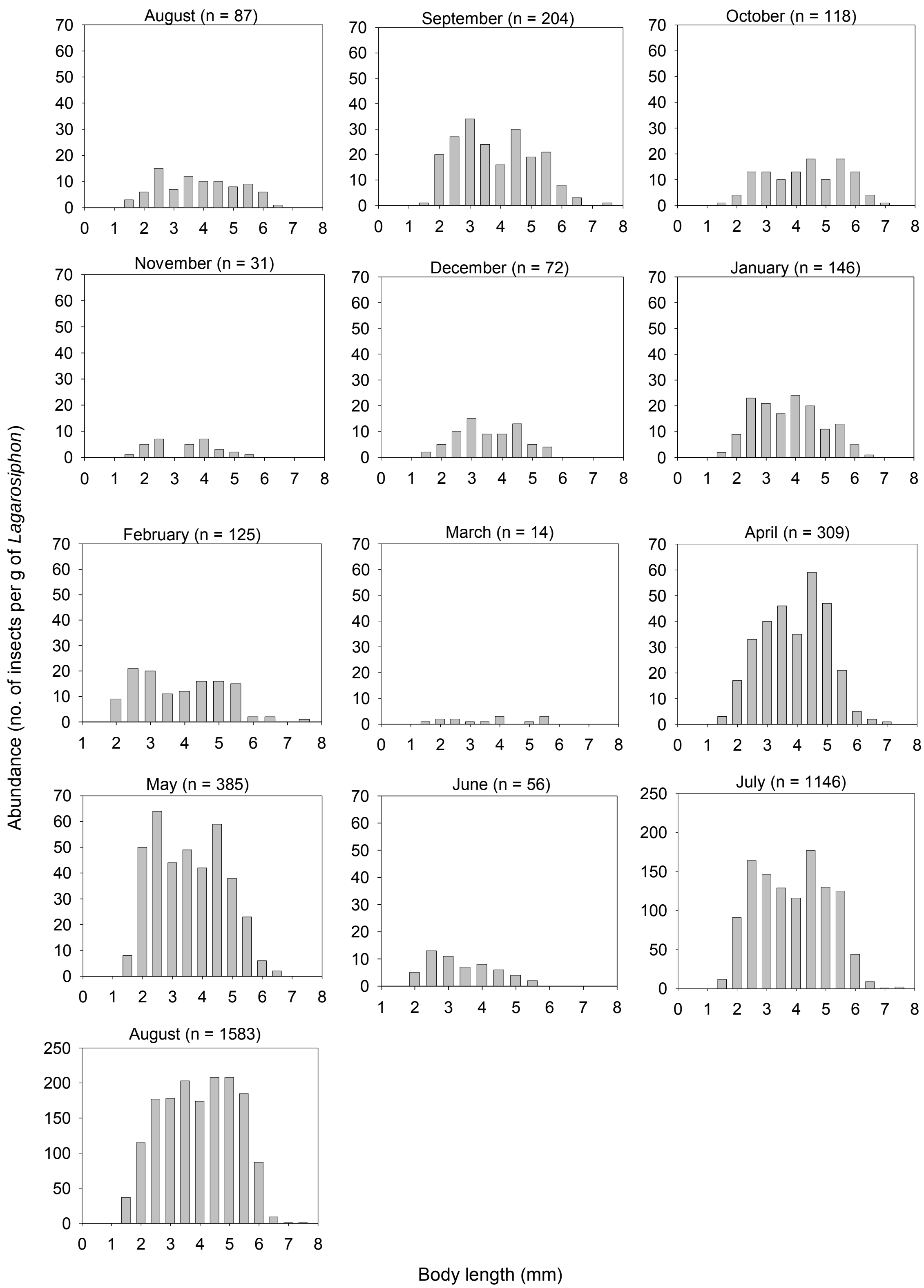

Figure 5.2. Body length distribution of *Cloeon* sp. **associated with** *Lagarosiphon* **in Lake Kariba from August 2007 to August 2008.**

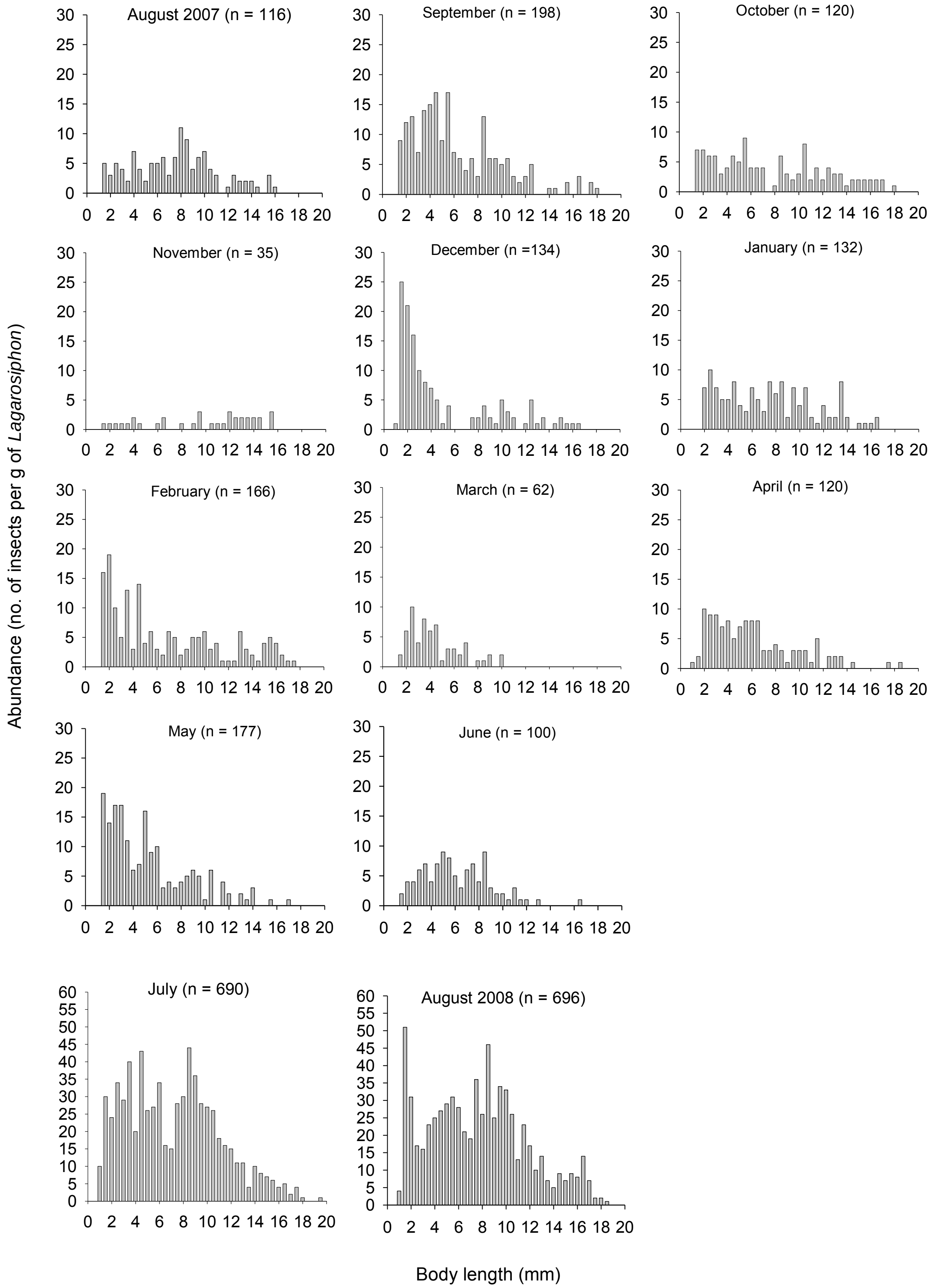

Figure 5.3. Body length distributions of Coenagrionidae naiads associated with *Lagarosiphon* in Lake Kariba from August 2007 to August 2008.

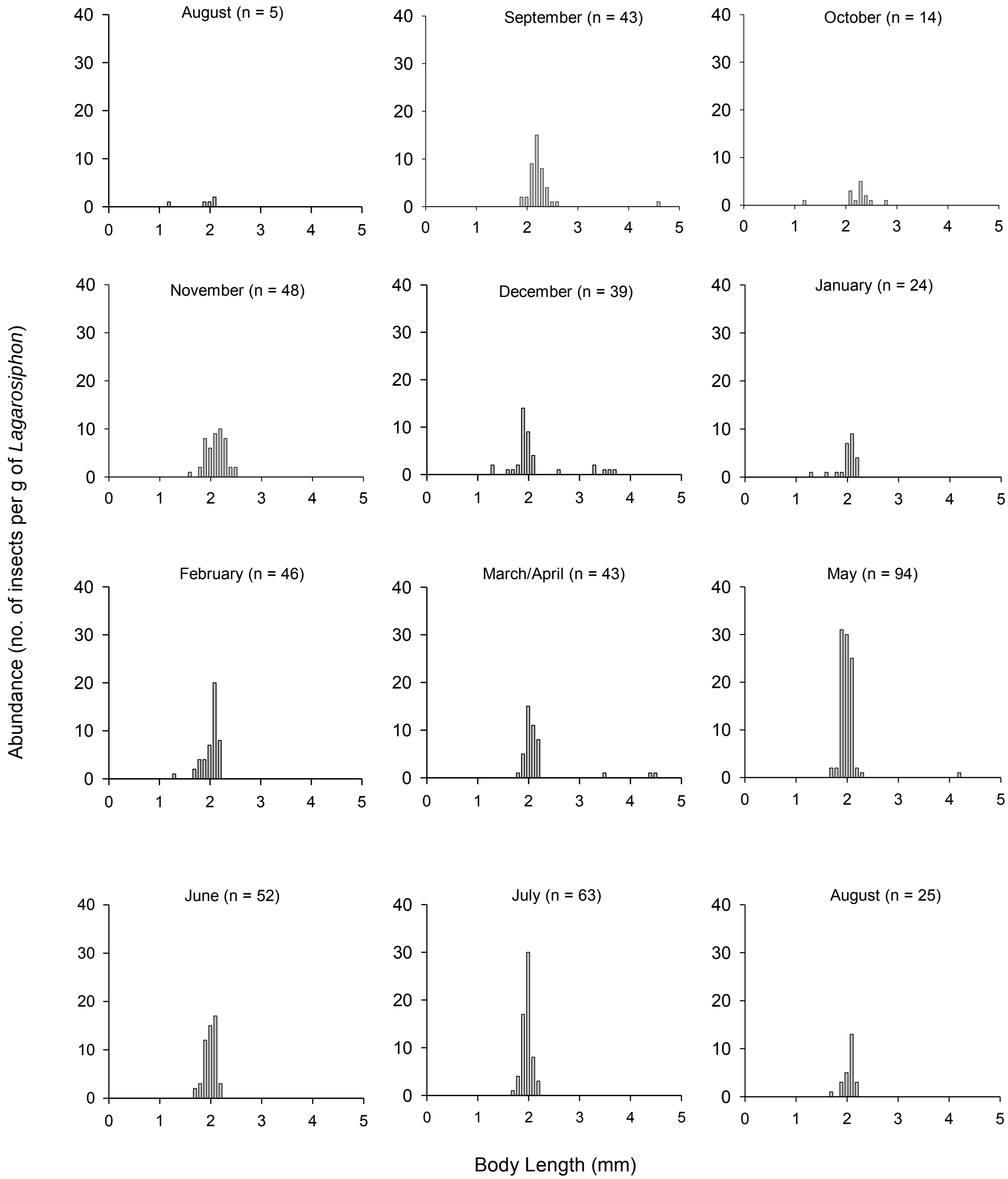

Figure 5.4. Body length distributions of *Micronecta* sp. **associated with** *Lagarosiphon* **in Lake Kariba from August 2007 to August 2008.**

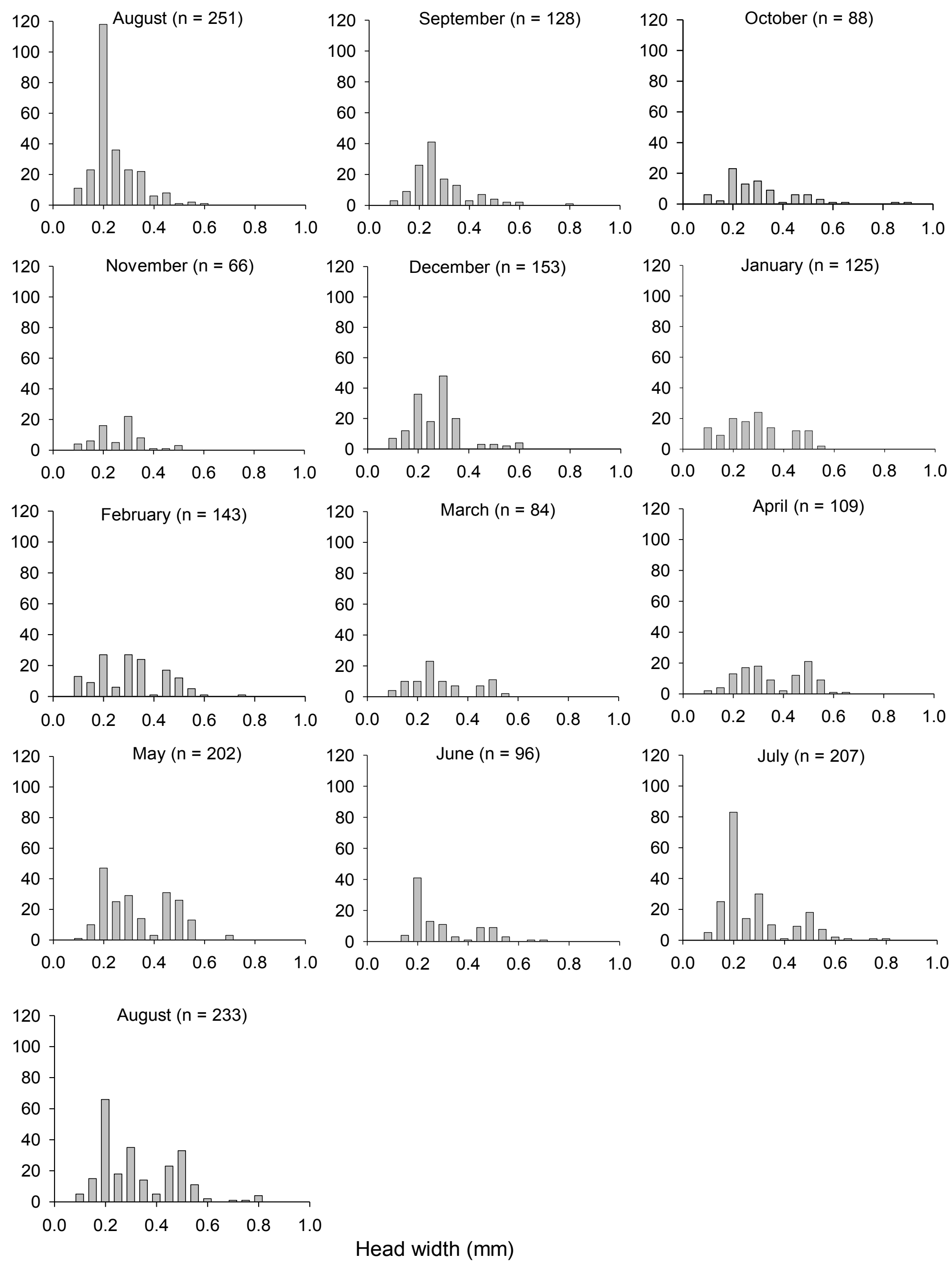

Figure 5.5. The head width distributions of Chironominae larvae associated with *Lagarosiphon* in Lake Kariba from August 2007 to August 2008.

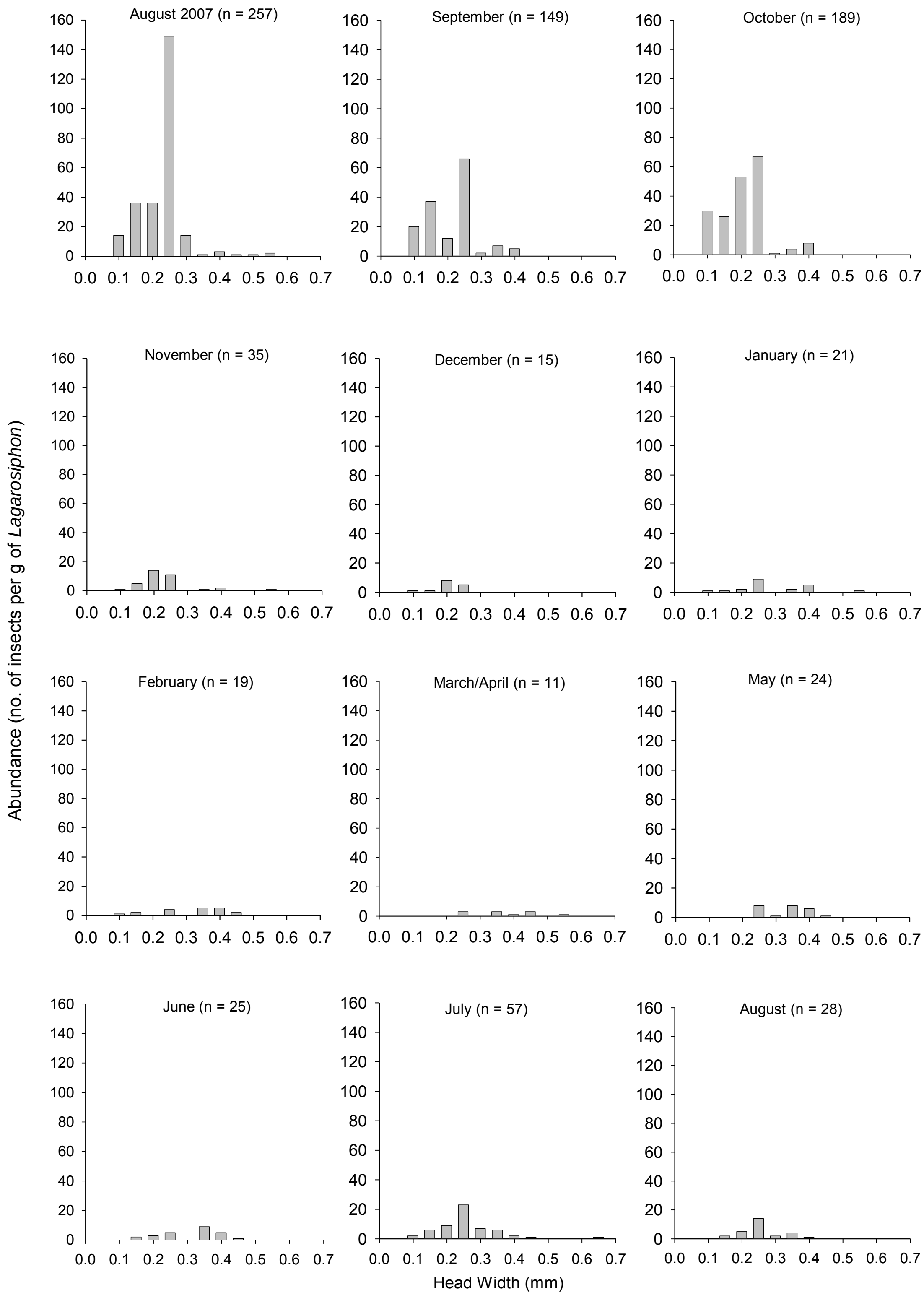

Figure 5.6. The head width frequency distribution of Orthocladiinae larvae associated with *Lagarosiphon* in Lake Kariba from August 2007 to August 2008.

5.3.2 *Cloeon* sp.

The size class distribution of *Cloeon* did not differ significantly throughout the sampling period (Kolmogorov-Smirnov test, $p > 0.05$). Analysis of body size distribution (Figure 5.2) and temporal variation in individual mean biomass (Figure 5.7) shows that the smallest sized individuals occurred in November and June. Figure 5.7 shows that mean individual body size generally decreased from August 2007 to November, increased gradually from December to February/March after which it gradually decreased up to June and increased thereafter. From August to November, hatching of eggs together with emergence and ovipositing resulted in the gradual decrease in average body size (Figure 5.7). Most of the eggs hatched in November resulting in low mean individual body size for the population (Figure 5.7). December to February was characterised by gradual increase in average individual body size (Figure 5.7) and overall *Cloeon* biomass (Figure 5.8) due to nymphal growth. Another period of relatively large scale emergence, mating and ovipositing of eggs occurred in March. The period from March to May was characterised by a gradual decrease in individual body size (Figure 5.7) as well as a gradual increase in overall population biomass (Figure 5.8) due also to emergence, ovipositing and hatching of some eggs. In July the hatching of comparatively large number of eggs was reflected by sharp increase in abundance (Chapter 4, Figure 4.3b), while increase in average body size (Figure 5.7) suggests rapid nymphal growth. Analysis of *Cloeon* abundances (Chapter 4), as well as body size and biomass distribution suggests a multivoltine life cycle with mating and ovipositing largely occurring in October/November, February/March and May/June.

Average *Cloeon* biomass (Figure 5.8) differed significantly among months (ANOVA, $F_{12,\ 37} = 9.657$, $p < 0.001$). From August 2007 to June, the biomass periodically decreased every two months, with low values obtained in November, December, March and June (Figure 5.8). Biomass in July and August (2008) was significantly greater than in August (2007), September, October, November, December, March, April, and June, while in January and May it was significantly greater than in November and June (Tukey Q tests, $p < 0.05$). Biomass in June was also significantly less than that in October, February and April (Tukey, Q tests, $p < 0.05$).

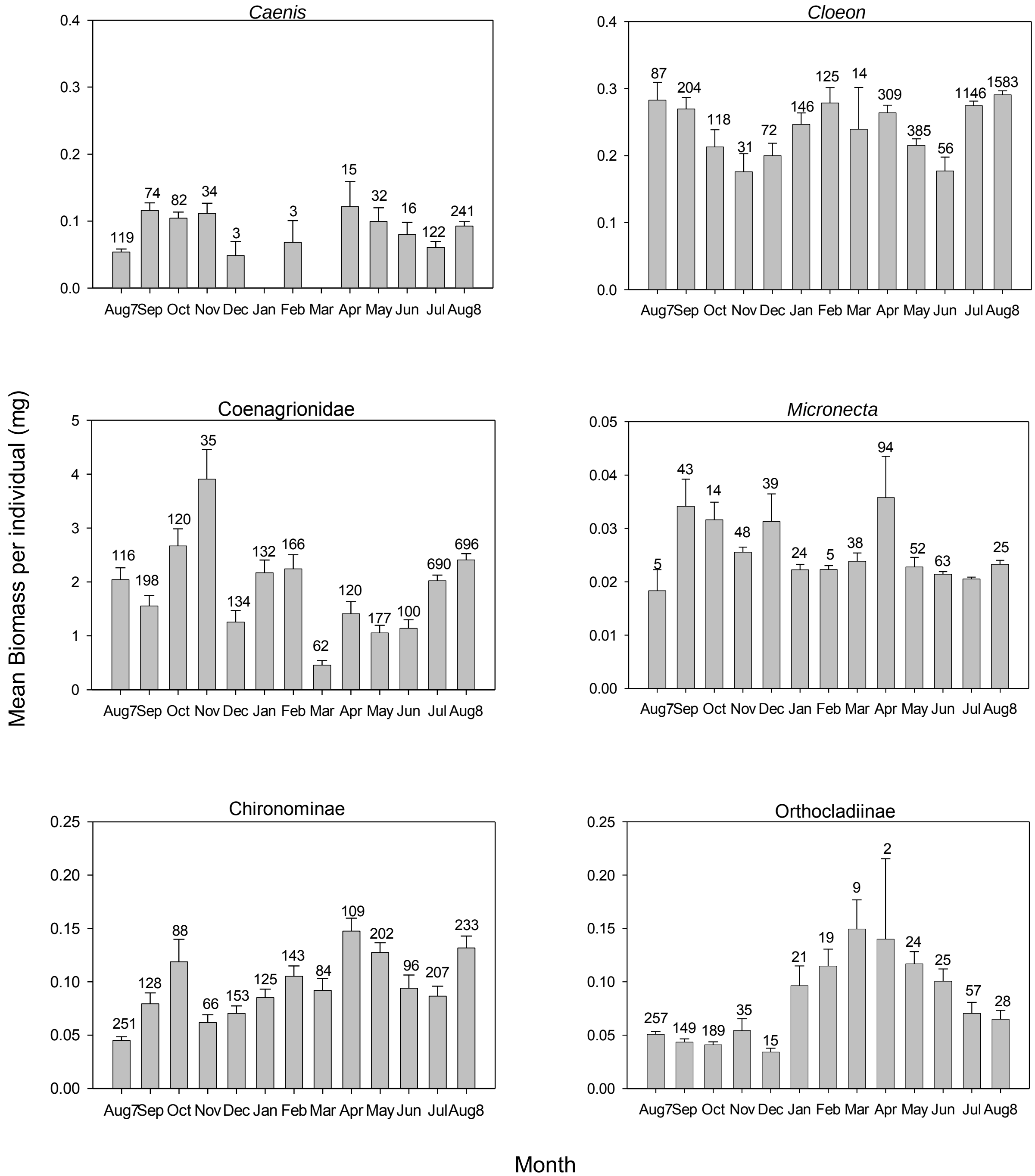

Figure 5.7. Temporal variation in means of individual dry mass of the six main insect taxa associated with *Lagarosiphon*. Error bars are standard deviations around the mean. The number shown above each bar is the number of insect that were measured for calculation of mean biomass.

5.3.3 Coenagrionidae

The lowest number of coenagrionid naiads was obtained in November at which time 54.3% had body sizes equal to or greater than 10mm. In October and November, 10.0% and 14.3% of the naiads respectively had body sizes greater than 14 mm, with well developed wing sheaths. Generally, mean body size of naiads steadily increased from August 2007 to November, and then dropped in December (Figure 5.7). Small-bodied naiads were collected in December (Figure 5.7) and a significantly greater proportion of small individuals was obtained in December compared to August 2007, September, October, November, January, February, April, July and August 2008 (Kolmogorov-Smirnov tests, $p < 0.05$). Significantly greater proportions of small naiads also occurred in March compared to August 2007, September, October, December, January, February, April, May, July and August 2008 (Kolmogorov-Smirnov tests, $p < 0.05$). In March, small to moderately sized naiads dominated and there were none with body size greater 10mm (Figure 5.3). This suggests that large scale emergence, mating, ovipositing and hatching of coenagrionid eggs mainly occurred between October and December, and in February/March. The presence of small bodied-naiads as well as large-bodied naiads with well developed wing sheaths throughout much of the study period also implies that conditions may have enabled some emergence, mating, and ovipositing and hatching of eggs to occur throughout the study period. Significant temporal differences were observed in the biomass of Coenagrionidae (ANOVA, $F = 5.13$, $p < 0.001$). The highest mean biomasses were obtained in the periods between November and February, as well as in July and August (2008) (Figure 5.8). The lowest biomass values were recorded in the period March to June. The biomass recorded in July was significantly greater than in September, October, December, March, April, May and June, while in January and August it was significant greater than in March, May and June (Tukey Q test, $p < 0.05$). The biomass in February was significant greater than in March and May, while in May biomass was also significantly less than in August (2007) and November (Tukey Q test, $p < 0.05$).

5.3.4 *Micronecta* sp.

The body size distribution of *Micronecta* had no distinct pattern during the thirteen-month period (Figures 5.4 and 5.7). The proportion of size classes did not differ significantly among months (Kolmogorov-Smirnov test, $p > 0.05$). Two peaks, in November and July (Figure 5.8), were observed in the biomass and there were significant differences among months (Kruskal Wallis ANOVA, F = 37.89, $p < 0.001$). The biomass of *Micronecta* in July was significantly greater than all the other months sampled (Wilcoxon Mann Whitney U tests, $p < 0.05$) with the exception of November. The biomass in November was significantly greater than in December, January, March, May and June (Wilcoxon Mann Whitney U tests, $p < 0.05$). *Micronecta* biomass in August 2007 was significantly less than in the period October to August 2008, while in September it was significantly less than in November, December, and the period Mach to August 2008. In October biomass was significantly less than in November and the period April to July (Wilcoxon Mann Whitney U tests, $p < 0.05$). Biomass in December was significantly less than in May, June and July, while in January it was significantly lower than in April, May, June, July and August 2008. Thus *Micronecta* biomass increased sharply from August 2007 to November, dropped sharply in December and January, increased in February and slightly decreased March (Figure 5.8). From April to May it gradually increased, decreased slightly in June, rose sharply in July and decreased once more in August 2008. The abundance (Chapter 4, Figure 4.3) and biomass trend suggest that *Micronecta* underwent at least two periods of rapid growth and emergence that is October/November and July/August 2008.

5.3.5 Chironominae

After slightly decreasing in September and October, mean abundance of Chironominae generally increased from November to May, decreased in June and sharply rose thereafter (Chapter 4, Figure 4.3c). The proportion of different size classes did not differ significantly among months (Kolmogorov-Smirnov test, $p > 0.05$) suggesting all year round reproduction. Mean body size increased from August 2007 to October and after a decrease in November, it gradually increased up to April and then gradually decreased until July (Figure 5.7). Although production occurred all year round, the mean individual body size pattern (Figure 5.7) suggests that emergence and ovipositing of eggs largely occurred in October/November and March/April, and most numbers of eggs hatched in November and July. The lowest mean population biomass was obtained in June (Figure 5.8), after which there was a considerable increase in July and August 2008. Significant differences in biomass occurred between some of the months (ANOVA, $F_{12, 37} = 27.64$, $p < 0.001$). No significant differences in biomass were observed from August 2007 to January (Tukey Q test, $p < 0.05$). July and August 2008 did not differ significantly with respect to Chironominae biomass (Tukey Q test, $p > 0.05$), but significantly greater biomass was obtained in August 2008 compared to all the other months, while July had significantly greater biomass than June and the period August 2007 to March (Tukey Q tests, $p < 0.05$). February had significantly greater biomass than September, October, November and June; April greater than August 2007, September, October, November, December and June; and May greater than August 2007, September, October, November and June (Tukey Q tests, $p < 0.05$). Thus from August 2007 to November there was relatively low standing crop of Chironominae associated with *Lagarosiphon*. Biomass gradually increased from December to May, sharply decreased in June, and increased considerably in July and August 2008 (Figure 5.8).

5.3.6 Orthocladiinae

Mean individual biomass of Orthocladiinae slightly but gradually decreased from August 2007 to December, rapidly increased up to March/April then underwent a gradual decrease thereafter (Figure 5.7). The head width size distribution was significantly different between August 2007 and December, with a greater proportion of larger size classes in August 2007 compared to December (Kolmogorov-Smirnov test, $D = 0.500$, $p = 0.016$). Interestingly, abundance gradually decreased from August 2007 to December and remained constantly low up to June, then sharply increased in July and August (Chapter 4, Figure 4.3c). The gradual decrease in numbers and individual body size between August 2007 and December suggests a period that was largely characterised by the hatching of eggs but low larval growth. Contrastingly, although mean body size gradually increased between December and April (Figure 5.7), abundances remained steadily low (Chapter 4, Figure 4.3c). This suggests that unlike the period between August and December, larval growth in the period December to April was comparatively fast. The gradual decrease in body size that occurred from April to August 2008 was possibly due to emergence and increase in the number of eggs that were hatching. A large number of eggs hatched in July/August 2008, during which the population consisting of small-bodied larvae (Figure 5.7) increased considerably in abundance (Chapter 4, Figure 4.3c). The data suggests that from August 2007 to November, some eggs hatched but there was virtually no larval growth (Figure 5.7) and numbers gradual decreased (Chapter 4, Figure 4.3c). Low abundances (Figure 4.3c) as well as low mean population biomasses (Figure 5.8) were maintained from December to June, during which period relatively rapid larval growth occurred (Figure 5.7). Large scale emergence and ovipositing then occurred in March/April and some eggs hatched between April and June. The sharp increase in abundance (Chapter 4, Figure 4.3c) of small-bodied larvae suggests that most eggs hatched in July and August 2008 (Figure 5.7).

Orthocladiinae population biomass gradually decreased from August 2007 to December (Figure 5.8). Between January and June, there was a marginal increase in the biomass, followed by drastic increase in July and August 2008 (Figure 5.8). Biomass differed significantly among some of the months (ANOVA, $F_{12, 37} = 11.92$, $p < 0.001$). The average biomass in July and August 2008 was generally similar (Tukey Q test, $p > 0.05$), but was significantly greater than in the period October to June (Tukey Q tests, $p < 0.05$). Biomass in August 2007 was significantly greater compared to November, December, January and April; that in September was significantly greater than in December and April, and the biomass in December was significantly lower than in October (Tukey Q tests, $p < 0.05$).

Thus generally all six insect taxa showed a significant temporal variation in biomass, with the highest mean biomass values for most taxa recorded towards the end of the sampling period in July/August 2008.

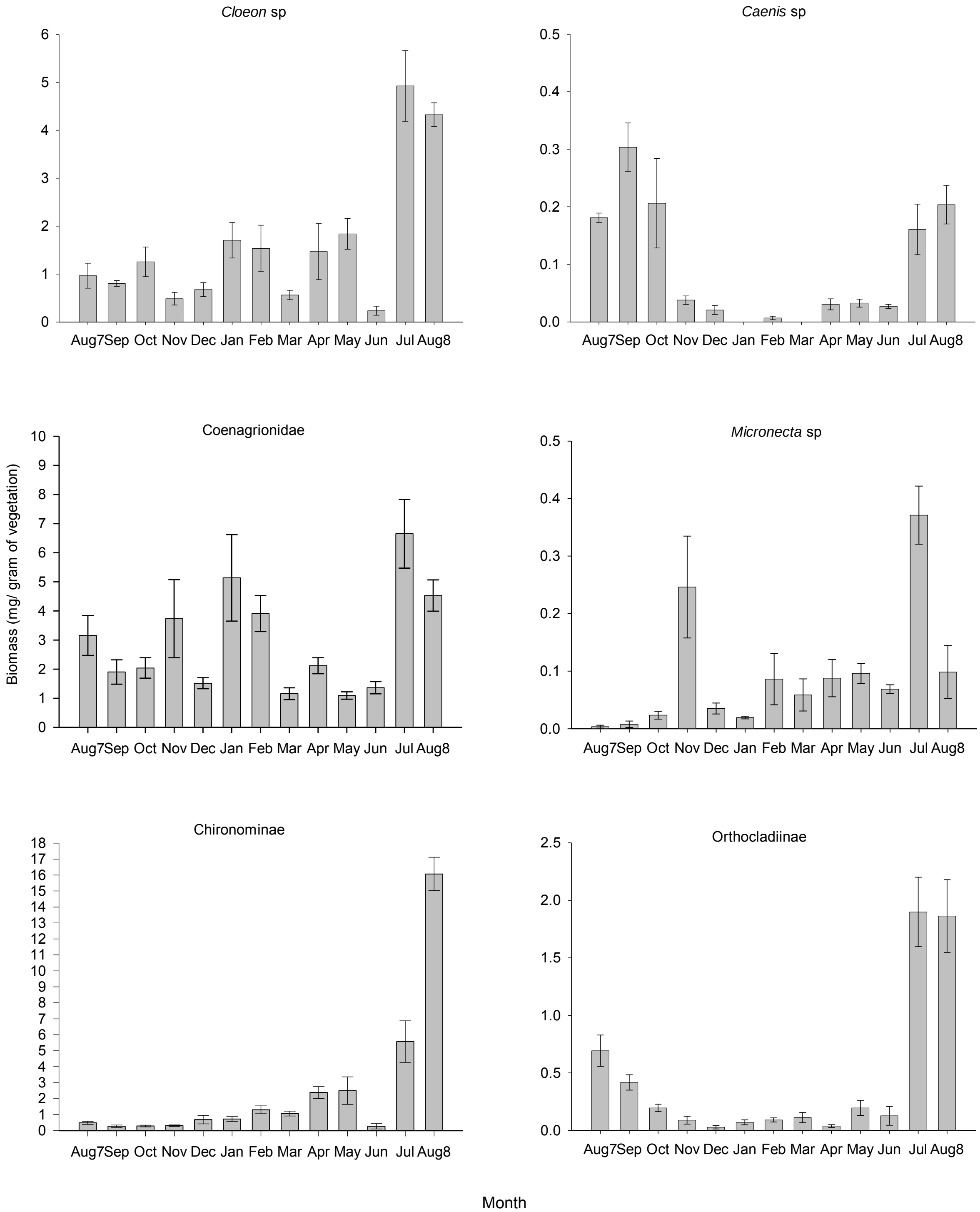

Figure 5.8. Temporal biomass distributions of the six most abundant insect taxa commonly associated *Lagarosiphon* in Lake Kariba. Error bars are ±1 standard error. Note the differences in scale on the y axis of the graphs.

5.3.7 Comparison of mean biomasses among the six insect taxa

Estimates of the mean biomass of each of the six insect taxa are shown in Table 5.1. The damselfly family, Coenagrionidae, comprising largely of *Ischnura* sp and *Pseudagrion* sp, had the highest biomass, followed by the chironomid subfamily Chironominae and the mayfly genus *Cloeon*. The mean biomass of Coenagrionidae was significantly greater than of the other taxa (Kruskal-Wallis ANOVA, $p < 0.05$) and there was no significant difference between *Cloeon* and *Chironominae* (Kruskal-Wallis ANOVA, $p > 0.05$). *Micronecta* had the lowest average biomass, which was significantly less than that of the other five taxa (Kruskal-Wallis ANOVA, $p < 0.05$).

5.3.8 Temporal variation in overall biomass of the six insect taxa

The overall average biomass of the six taxa was 8.36 ± 1.12 mg per gram dry mass of *Lagarosiphon*. Figure 5.9 shows temporal variation in overall biomass of the six insect taxa. Average total biomass differed significantly among months (ANOVA, $F_{12, 37} = 19.67$, $p < 0.001$). The largest average biomass values were obtained in July and August 2008. Average insect biomass in both July and August 2008 was significantly greater compared to all the other months (Tukey Q tests, $p < 0.05$). Total mean biomass in January was significantly greater than in December, March and June, while biomass in June was significantly lower than in August 2007, February, April and May (Tukey Q tests, $p < 0.05$). Figure 5.9 suggests that there was a near regular fluctuation in total insect biomass during the study period. After August 2007, there was a decrease in biomass in September, which was followed by an increase in October/November. In December, biomass decreased but rose in January/February only to decrease once more in March. Another increase in mean biomass in April/May was followed by a decrease in June and an increase in July/August. The data suggests a three months regular cycle of insect biomass, consisting of two months during which biomass is relatively high, followed by a month when it falls to a comparatively low value. Thus, although insect biomass production on *Lagarosiphon* occurs all year round, it is interspaced with periods of relatively low biomass when mass emergence, mating and ovipositing occurs, and periods of high biomass during which most eggs hatch, and larvae and nymphs undergo rapid growth.

5.3.9 Effect of water physicochemical variables

No significant correlations were recorded in the biomass of any of the insect taxa with pH, conductivity, and concentrations of phosphates, total nitrogen (TN) and nitrates (Table 5.2). The biomass of *Caenis* and Orthocladiinae were significantly and positively, and that of Chironominae was negatively correlated with total phosphorus concentration. A significant negative correlation was observed between *Caenis* and ammonium concentration. *Caenis* and Orthocladiinae were the only taxa whose biomass was negatively and significantly correlated with water temperature (Table 5.2). The biomass of *Caenis* was also significantly and positively correlated with dissolved oxygen, while those of *Micronecta* and Chironominae showed significant negative correlations with dissolved oxygen concentrations. *Cloeon*, *Micronecta,* Chironominae and Orthocladiinae all showed significant and positive correlations with water levels in the lake. Coenagrionidae was the only taxa whose biomass did not show any significant correlations with any of the water physicochemical variables. Total insect biomass was positively and significantly correlated with dam water level (Table 5.2). Thus, high water temperature had an adverse effect on biomass of *Caenis* and Orthocladiinae but had an insignificant effect on total insect biomass. Increase in water level in Lake Kariba, had a positive effect on the biomass of *Cloeon*, *Micronecta*, Chironominae and Orthocladiinae, and generally resulted in a significant increase in the biomass of aquatic insects associated with *Lagarosiphon*.

Table 5.1. The average biomass of the six most common and abundant insect taxa associated with *Lagarosiphon*. The average total biomass of the six taxa is also shown.

Taxa	Biomass (mg/ g dry mass of *Lagarosiphon*)
Cloeon sp	1.74 ± 0.22
Caenis sp	*0.11* ± *0.02*
Coenagrionidae	3.06 ± 0.31
Micronecta sp	0.10 ± 0.02
Chironominae	2.88 ± 0.68
Orthocladiinae	0.49 ± 0.10
Total mean biomass of the six taxa	8.36 ± 1.12

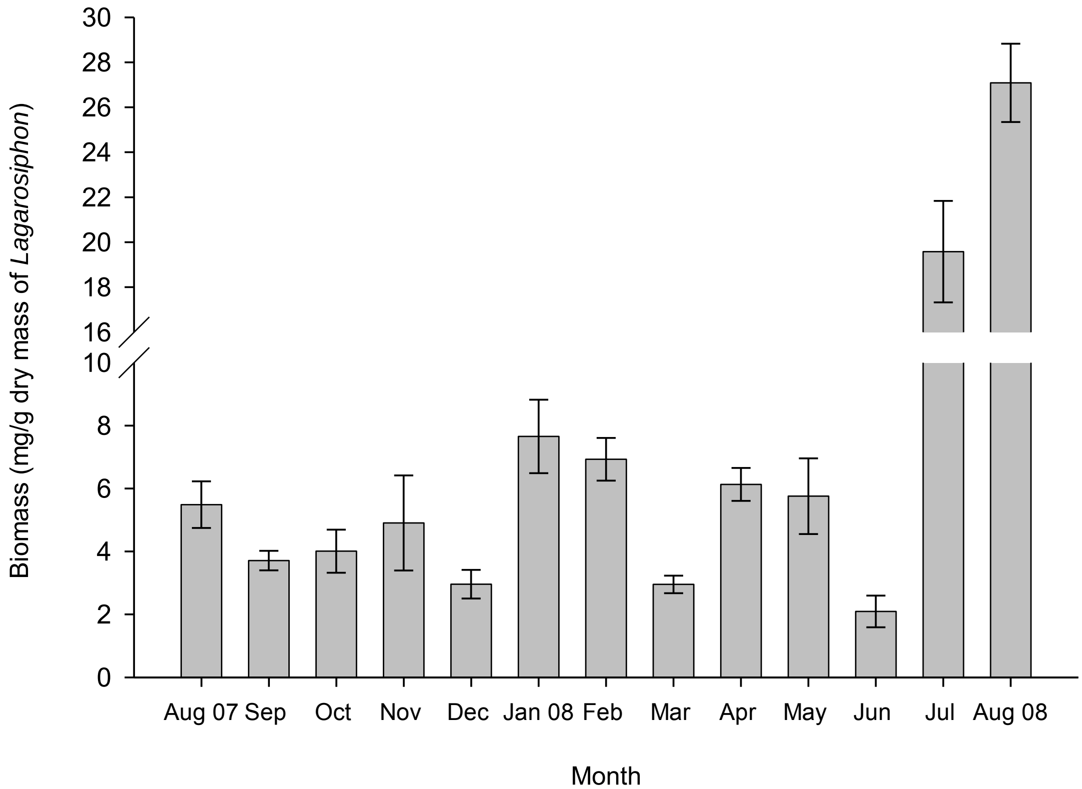

Figure 5.9. Temporal variation in total biomass of the common and most abundant insect taxa associated with *Lagarosiphon* in Lake Kariba

Table 5.2. Spearman correlation coefficients for the relationship between the biomasses of six insect taxa associated with *Lagarosiphon* and water physicochemical characteristics of in shallow waters of a bay on Lake Kariba. Significant correlations (*p* < 0.05) are presented in bold type.

	TP	PO_4^{3-}	TN	NH_4^+	NO_3^-	pH	Temperature	Conductivity	Turbidity	DO	Dam Level
Cloeon sp	-0.063	0.139	-0.088	0.291	0.098	0.126	-0.188	0.145	-0.252	-0.173	**0.373**
Caenis sp	**0.586**	-0.154	-0.116	**-0.490**	0.016	-0.036	**-0.644**	0.146	0.229	**0.341**	0.027
Coenagrionidae	-0.083	0.043	0.056	0.175	0.038	0.220	-0.230	-0.117	-0.183	0.151	-0.023
Micronecta sp	-0.339	-0.100	0.297	0.130	0.124	0.169	0.049	-0.095	-0.147	**-0.475**	**0.396**
Chironominae	**-0.460**	0.080	-0.194	0.244	-0.114	0.038	0.044	-0.017	**-0.294**	**-0.506**	**0.589**
Orthocladiinae	**0.404**	-0.173	-0.034	-0.346	-0.161	-0.085	**-0.653**	0.217	-0.277	0.072	**0.300**
Total biomass of the six insect taxa	-0.120	0.038	-0.095	0.227	0.026	0.112	-0.217	-0.005	-0.254	-0.139	**0.287**

5.4 Discussion

The analysis of temporal body size distribution suggests that five of the six major insect taxa associated with *Lagarosiphon* in Lake Kariba, that is, *Cloeon*, Coenagrionidae, *Micronecta* sp, Chironominae and Orthocaldiinae, have multivoltine life cycles. Multivoltine life cycles by aquatic insects characterized by asynchronous development and fast growth rates are widespread in tropical and subtropical systems (Brittain 1982, Benke & Jacobi 1986).

5.4.1 *Caenis* and *Cloeon*

Most mayflies have short life cycles (Brittain 1990) and according to Marchant (1982) and Benke & Jacobi (1986) some can complete their life cycle in less than 30 days. Many mayfly species, especially among the Baetidae, show life cycle plasticity and are able to change the number of generations per year in response to changes in temperature (Brittain 2008). The aquatic nymphal stage is the dominant life history stage, with nymphs undergoing a number of moults as they grow and the number may vary depending on a number of factors such as temperature and food availability (Brittain & Sartori 2003). In general, mayflies in warmer, subtropical or tropical regions are multivoltine, while those of temperate regions tend to be univoltine or semivoltine with seasonal traits (Clifford 1982). Bilvoltine (Clifford 1982, Mol 1983) and multivoltine (Christman & Voshell 1992, Perán *et al*. 1999) life cycles have been reported for some *Caenis* species. This study suggests that *Caenis* in Lake Kariba largely has a univoltine life cycle, with growth and recruitment mainly occurring between July and November. The presence of small numbers of nymphs between November and June implies that small numbers of eggs did hatch during this period, however most of the eggs hatched in July, which was associated with relatively low water temperatures, and both *Caenis* abundance (Chapter 4) and biomass were generally low at high water temperatures. This seems to support Clifford (1982) who suggested that although the life cycles of many *Caenis* species is quite flexible, the most common life cycle among *Caenis* species is univoltine with eggs hatching and growth occurring at relatively low temperatures. This study suggests that in Lake Kariba, *Caenis* growth and reproduction is generally restricted to water temperatures below the mid 20^{O}Cs. It can be argued from the observations that between November and June most of the *Caenis* eggs were possibly in diapause, an adaptation which according to Pritchard *et al.* (1996) is used by cold-adapted aquatic insects to survive periods of high temperature.

The baetid, *Cloeon*, had a characteristically multivoltine life cycle, with at least three generations noted during the study period. Many mayfly species show fast growth rates characteristic of multivoltine life cycles, especially in tropical and subtropical regions, as well as in areas where water temperature is greater than 15^{O}C for much of the year (Benke & Jacobi 1986). *Cloeon* abundance (Chapter 4) and biomass were positively and significantly correlated with water level, but were not significantly correlated with temperature. The occurrence of relatively large numbers of all size classes in each month suggests that, unlike the situation with regard to *Caenis*, temperature variation had little impact on *Cloeon* life cycle dynamics. This suggests that temperature did not limit growth and reproduction by *Cloeon* during much of the study period. Mayfly species show considerable differences in optimal temperature range and although a number of species have over 50% egg hatching success at temperatures above 25^{O}C (Brittain 1990), most hatch at temperatures in the range of 3 to 21^{O}C (Brittain & Sartori 2003). The current study suggests that water temperatures in the upper 20^{O}Cs inhibited *Caenis* growth and reproduction, while *Cloeon* was generally unaffected. The fact that water level fluctuation affected *Cloeon* abundance (Chapter 4) and biomass suggests that it is a key factor in the life cycle of the genus in Lake Kariba.

5.4.2 Coenagrionidae

Coenagrionid naiads were present throughout the study period, suggesting multivoltine life histories, with most of the emergence, mating, and ovipositing occurring in November, March and June. In Chapter 4, the abundances of *Pseudagrion* and *Ischnura* were shown to be significantly and positively correlated with water level, with *Pseudagrion* also significantly but negatively correlated with water temperature. This chapter shows that coenagrionid biomass was comparatively low from March to June, but the rise in temperatures between August and November was accompanied by an increase in mean body size and biomass. According to Pritchard *et al* (1996) warm-water coenagrionid species usually have high temperature optima for larval development, and generally the optimum temperature for odonate embryogenesis and hatching is between 30 and 35^{O}C. Pritchard (1982) and Pritchard & Leggott (1987) also noted that among odonates there usually is no egg development below about 10^{O}C and optimal temperatures for growth and activity of all life stages are above 20^{O}C. Odonate mating, which involves complex aerial manoeuvres, is also best accomplished in warm and sunny conditions (Pritchard *et al* 1996). Thus conditions in November, characterized by high water temperatures (average 29.2^{O}C, range 27.1 – 33^{O}C) were optimal for emergence, mating, ovipositing and hatching of eggs. A relatively large proportion of coenagrionid naiads collected in October and November were large-bodied with well developed wing sheaths. The relatively low abundances of coenagrionid naiads in November (Chapter 4) was probably due to emergence of relatively large numbers for mating. In December, there was an appreciable increase in abundance (Chapter 4) of small-bodied naiads which was due to the hatching of eggs. In March the coenagrionid assemblage was also dominated by small- to moderately-sized naiads suggestion another period during which a large number of eggs hatched. The study shows that there were two main periods during which large numbers of coenagrionid eggs hatched, that is November and March. The presence of most size classes throughout much of the study period also suggests that ovipositing and hatching of eggs continued for much of the thirteen month period. Thus the high water temperatures (mean 27.4^{O}C, range 22.0 – 33.0^{O}C) in the shallow water of the lake for the whole study period enabled continued growth and reproduction of coenagrionid species, enabling a multivoltine life cycle.

5.4.3 *Micronecta*

The corixid, *Micronecta*, had all year round growth and reproduction, with enhanced activity characterized by increased abundance (Chapter 4) and biomass, in November and July. The study suggests a largely bivoltine life cycle for *Micronecta*, with mating mainly occurring in November and July, and low levels of reproduction during the remaining months. *Micronecta* biomass increased as water levels rose in Lake Kariba.

5.4.4 Chironomids

Chironominae abundance was inversely related to water turbidity, and the concentrations of total phosphorus, total nitrogen, nitrates, and dissolved oxygen (Chapter 4). Biomass also significantly decreased with increase in the concentration of total phosphorus and dissolved oxygen, but increased with increase in water level. The abundance (Chapter 4) of Chironominae was positively correlated with the abundances of the coenagrionid naiads *Pseudagrion* and *Ischnura* (Chapter 4). Chironominae biomass was also positively and significantly related to the overall biomass of coenagrionid naiads. Chironomid larvae are preyed upon by coenagrionid naiads (Hilsenhoff 1991). Predatory invertebrates (Nyström & Åbjörnsson 2000), just like predatory fish (Diehl 1992, Nyström *et al.* 2001, Åbjörnsson *et al.* 2002), can have strong negative effects on prey abundances. In any given system predators generally feed on the most abundant prey species (Vázquez & Aizen 2003). Chironominae were the most abundant and dominant taxa on *Lagarosiphon* (Chapter 4) and so probably the most targeted prey species for invertebrate and fish predators. Thus the unexpected negative correlations between chironomin abundance and biomass, with nutrients and dissolved oxygen concentration, were possibly due to the effects of invertebrate and fish predation.

Mean chironomid abundance (Chapter 4) and biomass gradually increased from September to May, decreased in June and sharply increased in July and August 2008. Mean individual biomass increased from August to October, decreased in November, and then gradually increased from December to April. Between May and July individual body size steadily decreased, and rose in August. A broad range of head width size classes were present throughout the study period, implying year round reproduction. Chironomids in warm tropical and subtropical regions tend to be multivoltine (Ruiz *et al.* 2006). The generation time of a number of chironomid species usually decreases at high temperature (Nolte 1995, Balci 2002). Stevens (1998) found that the developmental rate of a chironomid, *Chironomus tepperi* Skuse, increased with increasing temperature from 12.5^{O}C to 32.5^{O}C, fell at 35^{O}C, and experienced low adult emergence at 37.5^{O}C. In the current study, the relatively high water temperatures (>20^{O}C) that occurred throughout the study period were probably favourable for continual chironomid reproduction and recruitment.

This study suggests that emergence, mating and ovipositing by Orthocladiinae, as well as hatching of eggs, occur throughout the year. Biomass and abundance (Chapter 4) were negatively correlated with temperature but positively affected by increase in water levels. Interestingly, mean individual body size was low from August 2007 to December a period that was characterised by increase in mean water temperatures (see Chapter 4, Figure 4.1). As temperatures stabilised in January/February and steadily decreased from February to August 2008 average body size also steadily increased from January to March then steadily decreased thereafter. Reist & Fischer (1987) and Kobayashi (1998) observed that the body size at maturation of some chironomid species decreased with increase in temperature at larval stages. The findings of this study suggests that between August 2007 and November as mean temperatures increased orthoclads were possibly maturing at small sizes and thus mean individual body size remained low. When temperatures stabilised from January to March, mean body size increased suggesting that larvae were maturing at larger sizes. Also interesting was the finding that as temperature decreased from March to August 2008, mean individual body size also steadily decreased. The study suggests that orthoclad reproduction in Lake Kariba occur all year round but periods of rapidly changing temperature are characterised by small size at maturation.

5.4.5 Overall biomass of the six insect taxa and comparisons with earlier studies

Total insect biomass was dominated by coenagrionid naiads and chironomine larvae. Generally, abundances of *Cloeon*, *Micronecta*, Chironominae and Orthocladinae were greater than those Coenagrionidae during the study period (CHAPTER 4). The mean abundances of Chironominae and Orthocladiinae were more than three-fold and twice as much as that of Coenagrionidae respectively. Chironomidae larvae often are among the numerically dominant benthic macroinvertebrates (Tokeshi 1995). Chironomid larvae occur abundantly on aquatic plants (Pardue & Webb 1985) and many studies have reported the numerical (e.g., Albertoni *et al.* 2007, Balcombe *et al.* 2007, Kratzer & Batzer 2007) and gravimetric (e.g., McLachlan 1969a, 1970b, Bowmaker 1973) dominance of chironomid larvae in epiphytic macroinvertebrate communities. Although damselfly nymphs are common in epiphytic macroinvertebrate communities of the littoral zones of lakes (Miller *et al.* 1989, Bergey *et al*. 1992) and have relatively large body sizes the overall gravimetric dominance of Coenagrionidae (Table 5.1) was unexpected. The original expectation on the basis of abundances was that Chironominae would dominate the biomass estimates of insect community associated with *Lagarosiphon*.

In earlier studies, McLachlan (1969a) and Bowmaker (1973) found that chironomids dominated the macroinvertebrate community associated with macrophytes of Lake Kariba. McLachlan (1968) and McLachlan & McLachlan (1971) estimated a benthic macroinvertebrate biomass of between 0.1 – 0.3 gm^{-2}, of which the Chironomidae made up more 70%. Chironomids were also the most numerically abundant taxa on submerged trees (McLachlan 1970b). In all the early studies on Lake Kariba macroinvertebrates, chironomids dominated numerically as well as in terms of biomass in the mud (McLachlan 1968), aquatic vegetation (McLachlan 1969a, Bowmaker 1973) and submerged tress (McLachlan 1970b). In all these early studies very little mention is made of zygopteran odonates, suggesting they had minimal numerical and biomass contribution to the macroinvertebrate community. The current study implies that the importance of zygopteran odonates in Lake Kariba has increased since the late 1960s and early 1970s. This is probably largely due to increase in submerged macrophyte cover that has occurred in the lake after the demise of the free floating macrophyte *Salvinia molesta*.

Coenagrionid naiads were the most abundant large insect predator associated with *Lagarosiphon*. They are generalist predators and feed on a wide variety of prey

(Lombardo 1997) including insects, oligochaetes, small crustaceans and molluscs (Hilsenhoff 1991) and sometimes on larval fish (Horn *et al.* 1994). They also make up part of the insect food base of a number of fish species (Corbet 1980, Crowder & Cooper 1982). Hilsenhoff (1991) suggests that due to their relatively large size and broad range of prey coenagrionid nymphs play an important role in the invertebrate food webs. Thus coenagrionid nymphs, as the most abundant large insect predators associated with *Lagarosiphon* in Lake Kariba have an important role in the food-web dynamics of the littoral zones of the lake, and especially on the abundance and biomass of other epiphytic macroinvertebrate taxa.

5.4.6 Effect of water physicochemical variables

The variations in water pH, conductivity, turbidity, concentrations of phosphates, total nitrogen and nitrates generally did not have significant effects on biomass of any of the insect taxa. Water temperature is an important factor in the development of aquatic insects and affects processes such as hatching time of eggs (Alba-Tercedor 1990), feeding rates and metabolism (Wotton 1995), larval development, adult size and fecundity (Sweeney & Vannote 1978, Sweeney 1984). The water temperature range (22.0 and 33^{O}C) for the study period reflected subtropical conditions, which are characterized by minimal seasonality. Such water temperature conditions should enable aquatic insect production and growth throughout much of the year, and so most of the insect taxa in this study showed a multivoltine life cycle, with more or less continual reproduction throughout the study period.

Thus, due to the relatively high water temperatures throughout the study period, the expectation was that biomass of none of the insect would generally be affected by variation in water temperature. The study though shows that high water temperature was accompanied by a significant decrease in the biomass of *Caenis* and Orthocladiinae. According to Newbold *et al.* (1994) water temperature plays an important role in governing mayfly life histories. Of the two mayfly taxa commonly associated with *Lagarosiphon* in Lake Kariba, *Cloeon* and *Caenis*, the study suggests that life cycle and biomass of the later was impacted by variation in temperatures.

Caenis growth and reproduction was limited to periods of comparatively low temperatures. The biomass of *Caenis* also decreased with at relatively high ammonium concentrations and increased with increase in the concentrations of total phosphorous and oxygen. Thus, *Caenis* was the quite sensitive to variation in water physicochemical conditions.

An increase in water levels in the lake was associated with relatively high biomass of *Cloeon*, *Micronecta*, *Chironominae* and *Orthocladiinae*. McLachlan (1969d, 1970a) also found that the biomass of chironomid larvae in shallow waters of the lake increased with rising water levels. Water level fluctuations have been shown to be a major factor in structuring the littoral zone flora and fauna of lakes and reservoirs (e.g., Osborne *et al.* 1987, Maceina 1993, Johnson *et al*. 2007). The flooding of near shore areas as water levels increase may result in uptake of nutrients from the flooded area into the water column, resulting in localized increase in primary production. Maceina (1993) found a positive relationship between lake water levels and chlorophyll *a* concentrations in the littoral and littoral:pelagic boundary region of Lake Okeechobee in Florida (USA). The increase in primary production should favour reproduction and growth of primary consumers. Thus, the positive association in the biomass of *Cloeon*, *Micronecta*, Chironominae and Orthocladiinae with increasing lake levels may have been due to increase in availability of food items for the insects. Water level fluctuation is therefore an important component of biomass production of insect taxa associated with *Lagarosiphon* in the shallow marginal waters of Lake Kariba.

5.4.7 Comment on the use of length-mass regressions for invertebrate biomass determination

The results presented here, especially on insect biomass, should be interpreted with caution. The determination of invertebrate biomass can be done using direct weighing of fresh, frozen or preserved animals, by biovolume determination or by length-mass conversion (Burgherr & Meyer 1997, Benke *et al.* 1999). Length-mass relations are widely used because they are less time consuming than direct weighing of organisms (Burgherr & Meyer 1997), they prevent biases caused by mass losses of preserved animals (Heise *et al*. 1988, González *et al*. 2002) and they make possible further work with stored samples (Towers *et al* 1994). Although the importance of length-dry mass relationships is well known, most of the data available for aquatic macroinvertebrates are from temperate habitats and very little from tropical and subtropical regions. In this study, length-mass regressions that were used were obtained from the work that has been done in south-eastern United States (see Benke *et al.* 1999). The transferability of length mass relationships among different regions is an issue that is still under debate. This is because differences have been observed in length-mass relationships for populations of the same species in different locations (Griffith *et al.* 1993, Burgherr & Meyer 1997). The differences may be due to differences in the physical and chemical environment (Burgherr & Meyer 1997, Benke *et al*. 1999), food availability (Gee 1988, Basset & Glazier 1995), and trophic conditions among different regions (Benke *et al*. 1999). Benke *et al.* (1999) though also state that differences in length-mass regressions of the same taxa in different regions may also occur due to investigator related biases in weighing or measurement rather than geographic location. Thus although the length-mass regressions used in this study were not developed in the southern Africa I assumed that there was a constant error since they were obtained from the same source and region. Although not absolutely correct the regressions were therefore useful for comparative purposes.

5.4.8 Conclusion

The current study suggests that multivoltine life cycles are the most common life histories of most insect taxa associated with *Lagarosiphon* in shallow waters of Lake Kariba. Although abundances are dominated by Chironomidae (Chapter 4), this study showed that insect biomass was dominated by coenagrionid naiads. In Chapter 4 it was shown that temperature was inversely correlated with the abundances of a number of invertebrate taxa and overall invertebrate abundance. In the current chapter the biomasses of only two insect taxa, *Caenis* and Orthacladiinae were significantly and inversely correlated with temperature but the total insect biomass was not significantly correlated with temperature. The biomass of *Cloeon*, *Micronecta*, Chironominae and Orthocladiinae, and total insect biomass significantly increased at high water levels. Thus Chapters 4 and 5 suggest that water temperatures and dam water level are important factors in structuring invertebrate assemblages associated with *Lagarosiphon*.

Among biotic interactions, fish predation has been shown to be one of the main factors that significantly impacts on invertebrate assemblage structure (e.g., Rennie & Jackson 2005). In the littoral zones of temperate lakes, habitat complexity provided by aquatic vegetation has been shown to reduce fish predation on invertebrates. In Chapter 6 I explore the effect of variation in the density of *Lagarosiphon* on epiphytic invertebrate assemblages to determine whether the effect of fish predation differs with vegetation density.

CHAPTER 6

THE EFFECT OF PLANT DENSITY ON EPIPHYTIC MACROINVERTEBRATES ASSOCIATED WITH *Lagarosiphon*

6.1 Introduction

The structure and heterogeneity of aquatic habitats affects the composition of aquatic organisms. Generally, areas that are structurally complex usually support greater abundance, biomass and diversity of invertebrates (Blindow *et al.* 1993) and vertebrates (Diehl & Kornijów 1998). Macrophytes enhance the physical and chemical heterogeneity in aquatic ecosystems. A number of characteristics of macrophytes have been used to quantify habitat complexity, including the type and number of plant species (Dionne & Folt 1991), complexity of plant morphology (Kershner & Lodge 1990), plant biomass (Cyr & Downing 1988a, b), plant density (Duarte & Kalff 1990) and plant surface area (Brown *et al.* 1988, Taniguchi *et al.* 2003).

Tolonen *et al.* (2003) suggested that aquatic habitat complexity in littoral zones of lakes is positively correlated with increase in the density of macrophytes. Studies have shown that increase in littoral zone vegetation density is associated with changes in invertebrate body size distribution, with large-bodied individuals and taxa generally more abundant in dense vegetation. This has been attributed to reduction in predation efficiency and foraging success of fish on invertebrates with increasing vegetation density (Dibble *et al.* 1996, Tolonen *et al.* 2003). In tropical and subtropical lakes this effect has generally not been observed probably because very high numbers of juvenile fish and small fish species are usually associated with macrophyte beds (Meschiatti *et al.* 2000, Iglesias *et al.* 2007), which tend to exert intense predation pressure on invertebrates associated with macrophytes (Jeppesen *et al.* 2007).

Lagarosiphon ilicifolius is the most abundant and widespread submerged aquatic plant species in Lake Kariba and therefore makes a significant contribution to the primary production and ecosystem functioning of the lake. Although *Lagarosiphon* is an important component of the Lake Kariba ecosystem, much remains unknown about its influence on macroinvertebrate and fish communities.

The objective of this study was to examine the effect of differing densities of *Lagarosiphon* on the epiphytic macroinvertebrate community structure of Lake Kariba. The study compared the species richness, diversity, total abundance, and the abundances of some of the taxa, and size class distributions of *Cloeon* (Ephemeroptera, Baetidae) and Coenagrionidae (*Pseudagrion*, *Enallagma* and *Ischnura*) in low, moderate and high-density beds of *Lagarosiphon*. I especially expected that low-density beds would differ markedly in macroinvertebrate composition from moderate and high density beds. These expectations were based on the assumptions that directly follow from the hypothesis that the top-down effects of fish predators are strongest in the simplest of habitats (Bechara *et al*. 1992). The hypotheses tested are that variation in the density of *Lagarosiphon* will result in: (1) differences in epiphytic macroinvertebrate richness, diversity, and total abundance and (2) differences in body size class distribution of *Cloeon* and the Coenagrionidae.

6.2 Materials and Methods

The study was carried out over a period of three weeks in September and October 2008. Invertebrate samples associated with monospecific beds of *Lagarosiphon* were collected weekly from the shallow waters (0.5m to 1m) of a bay (Site 6, Figure 2.1) on Lake Kariba. A qualitative method was used to categorise *Lagarosiphon* beds into low (at most five individual plants within $1m^2$), moderate (vegetation uniformly covering $1m^2$ with much of the lake bottom visible from above) high ($1m^2$ segment completely covered and bottom of lake not visible from above) density bed. The materials and methods that were used are described in detail in section 2.3.4.

6.3 Results

6.3.1 Water physicochemical conditions

Water temperature (ANOVA, $F_{2,\ 17}$ = 1.472, p = 0.257) conductivity (ANOVA, $F_{2,\ 17}$ = 1.513, p = 0.249), pH (ANOVA, $F_{2,\ 17}$ = 2.869, p = 0.084) and dissolved oxygen percent saturation (Kruskal-Wallis ANOVA, $F_{2,\ 17}$ = 0.847, p = 0.655) did not differ significantly different among the three vegetation density categories at the site (Table 6.1). There was though, a gradual but slight increase in pH with increase in vegetation density.

Table 6.1. The means (±standard error) of physicochemical variables in low, moderate and high-density beds of *Lagarosiphon* during study period (September – October 2008).

	Low-density (n = 6)	Moderate-density (n = 6)	High-density (n = 8)
Oxygen (%sat)	109.5 ± 1.5	113.8 ± 3.1	114.5 ± 5.2
pH	8.31 ± 0.03	8.37 ± 0.05	8.65 ± 0.10
Temperature (^{O}C)	27.8 ± 0.6	28.0 ± 0.8	29.5 ± 0.9
Conductivity (μS/cm)	101.5 ± 0.2	101.0 ± 0.2	101.6 ± 0.6

6.3.2 Macrophyte biomass

The average dry mass of vegetation sampled from low-density, moderate-density and high-density beds was 7.03 ± 1.27g, 13.65 ± 0.88g and 18.15 ± 0.69g respectively. The vegetation biomass sampled from the three density categories was significantly different (ANOVA, $F_{2,\ 6}$ = 32.77, p < 0.001). The average dry mass of vegetation sampled from high-density beds was significantly greater than from low and moderate beds, and that sampled from moderate-density beds was significantly greater than from low-density beds (Tukey Q multiple comparison tests, $p < 0.05$).

6.3.3 Macroinvertebrate communities and vegetation density

Overall, 42 macroinvertebrate taxa were collected, of which 31 were identified to generic level (Table 6.2). Twenty-one taxa occurred in more than 50% of the samples. The ten dominant taxa in terms of abundance made up 94.8% of total abundance and comprised of Ostracoda (31.0%), *Cyclestheria hislopi* (19.6%), Chironominae (15.5%), Oligochaeta (7.4%), *Dugesia* (6.0%), *Physa acuta* (4.8%), Orthocladiinae (3.5%), *Cloeon* (3.1%), *Ceriodaphnia* (2.7%) and Tanypodinae (1.2%) (Table 6.2). The mean abundances of each of the ten dominant taxa did not significantly differ among the three vegetation density classes (ANOVA, $p > 0.05$).

Mean total macroinvertebrate abundances ranged from 373 ± 131.8 organisms/g of *Lagarosiphon* dry mass (DM) in high-density beds to 434 ± 51.2 organisms/g DM of vegetation in moderate-density beds (Table 6.3). The overall mean macroinvertebrate abundance was not significantly different among the three density categories (ANOVA, $F_{2,\,6} = 0.123$, $p = 0.886$). The overall macroinvertebrate abundance and those of the individual taxa were not significantly correlated to the vegetation dry mass or water physicochemical variables (Pearson correlation, $p > 0.05$). The number of taxa and Shannon diversity index of the macroinvertebrate assemblages were not significantly different among the three vegetation density beds (ANOVA, $p > 0.05$) (Table 6.3).

Table 6.2. Average abundances (no. of organism per gram dry mass of *Lagarosiphon*) of macroinvertebrate taxa in low-, moderate- and high-density beds. The percent contributions of individual taxa to total macroinvertebrate abundance in each vegetation density category are shown in brackets. The percent contribution to the overall macroinvertebrate abundance (%abun) and frequency of occurrence (%freq) of each taxon are also presented; √ = present in low numbers (< 1% of total abundance).

Order	Taxa	Low (n=3)	Moderate (n=3)	High (n=3)	% abun	% freq
Rhynchobdellida	*Dugesia* sp.	16.5 (4.0)	23.3 (5.4)	33.8 (9.1)	6.0	100.0
Oligochaeta	Oligochaeta	28.2 (6.8)	40.0 (9.2)	21.9 (5.9)	7.4	100.0
Hirudinae	Glossiphonidae	√			√	9.1
Gastropoda	*Lobogenes* sp.		√		√	22.2
	Lymnaea columella	√			√	22.2
	Physa acuta	18.6 (4.5)	17.9 (4.1)	22.2 (5.9)	4.8	100.0
	Bulinus spp.	4.0 (1.0)	2.9 (0.7)	√	√	55.6
	Cleopatra sp.	√	√	√	√	44.4
	Ferrisia sp.		√		√	11.1
Hydracarina	Acari	1.5 (0.4)	0.9 (0.2)	2.8 (0.7)	√	100.0
Cladocera	*Daphnia* sp.	8.4 (2.0)			√	11.1
	Chydorus sp.	√	√	√	√	33.3
	Ceriodaphnia sp.	23.1 (5.5)	6.9 (1.6)	3.0 (0.8)	2.7	66.7
Ostracoda	Ostracoda	148.3 (35.5)	153.8 (35.4)	77.8 (20.9)	31.0	100.0
Calanoida	Calanoida	1.3 (0.3)	√		√	44.4
Cyclopoida	Cyclopoida	√	√	1.1 (0.3)	√	66.7
Conchostraca	*Cyclestheria hislopi*	84.5 (20.3)	72.3 (16.7)	83.0 (22.2)	19.6	66.7
Decapoda	*Caridina nilotica*	√	√	√	√	100.0
Collembolla	Collembola			√	√	11.1
Ephemeroptera	*Caenis* sp.	√	√		√	22.2
	Cloeon sp.	12.6 (3.0)	12.1 (2.8)	13.5 (3.6)	3.1	100.0

Table 6.2. Continued

Order	Taxa	Low (n=3)	Moderate (n=3)	High (n=3)	% abun	% freq
Odonata	*Pseudagrion* sp.	2.7 (0.7)	2.0 (0.5)	√	√	88.9
	Enallagma sp.	1.4 (0.3)	√	1.6 (0.4)	√	55.6
	Ischnura sp.	√	√	1.0 (0.3)	√	100.0
	Coenagrionidae*	2.8 (0.6)	3.5 (0.1)	3.3 (0.9)	√	100.0
	Anax sp.		√	√		22.2
	Libellulidae			√	√	11.1
Hemiptera	*Eurymetra* sp.		√	√	√	33.3
	Micronecta sp.	1.3 (0.3)	√	√	√	55.6
	Nychia sp.		√	√	√	22.2
	Anisops sp.		√	√	√	33.3
	Plea sp.	√			√	11.1
	Appasus sp.		√			11.1
Trichoptera	*Orthotrichia* sp.	2.7 (0.6)	1.5 (0.4)	1.9 (0.5)	√	100.0
	Ecnomus thomasetti	1.3 (0.3)	√	√	√	77.8
Coleoptera	Dysticidae			√		9.1
Diptera	*Bezzia* sp.		√	1.5 (0.4)	√	33.3
	Culicoides		√			11.1
	Chaoborus sp.	√			√	22.2
	Chironominae	38.2 (9.2)	70.8 (16.3)	80.7 (21.2)	15.5	100.0
	Tanypodinae	10.4 (2.5)	4.1 (0.9)	√	1.2	66.7
	Orthocladiinae	7.0 (1.7)	17.3 (4.0)	18.9 (5.1)	3.5	100.0
	Culex sp.	√			√	11.1

*Unidentified Coenagrionidae, largely small first instar specimens

Table 6.3. The average (± standard error) of the total macroinvertebrate abundance, number of taxa and Shannon diversity index of epiphytic macroinvertebrates on *Lagarosiphon* at three levels of vegetation density. The P values of ANOVA for each variable are shown.

Index	Vegetation Density			P
	Low (n = 3)	**Moderate (n = 3)**	**High (n = 3)**	
Total abundance	417.3 ± 66.4	434.0 ± 51.2	373 ± 131.8	0.89
Number of Taxa	22.0 ± 2.5	23.3 ± 1.7	22.3 ± 1.5	0.89
Shannon diversity	2.74 ± 0.16	2.68 ± 0.17	2.71 ± 0.06	0.94

Non-metric multidimensional scaling based on 21 of the most the frequently occurring and abundant taxa showed no separation of macroinvertebrate community structure on the basis of differing vegetation density (Figure 6.1). Cluster Analysis showed that on each sampling date the similarity in macroinvertebrate community composition for the three vegetation density categories was more than 80%, while the overall similarity for all samples was about 70% (Figure 6.2). Thus during the study period macroinvertebrate assemblage structure associated with low, moderate and high-density beds of *Lagarosiphon* were relatively similar, and there were no significant differences among the three vegetation density categories in macroinvertebrate assemblage composition (ANOSIM, Global R = -0.169; p = 0.754).

6.3.4 Macroinvertebrate functional feeding groups and vegetation density

Collector-gatherers and collector-filterers dominated the functional feeding group representation in all three vegetation density categories (Figure 6.3) and made up more than 80% of the macroinvertebrate abundance in each category. In low-density and moderate-density beds, collector-gatherers comprised more than 60% of macroinvertebrate composition, while collector-filterers made up slightly more than

20% of the community (Figure 6.3). The contribution of collector-gatherers slightly decreased to about 45% while that of collector filterers increased to about 35% of macroinvertebrate abundance in high-density vegetation beds. There were no significant differences in the average abundance of collector-gatherers and filterers in each of the three vegetation density categories and both functional groups did not differ significantly among the three vegetation categories (ANOVA, $p > 0.05$). The average predator to total macroinvertebrate abundance ratio ranged from about 8% in moderate to 10% in high vegetation density groups, while the grazer ratio underwent slight increase from about 6% in low and moderate beds to just fewer than 10% in high density beds (Figure 6.3). None of the functional groups underwent a significant change in abundance with change in vegetation density (ANOVA, $p > 0.05$).

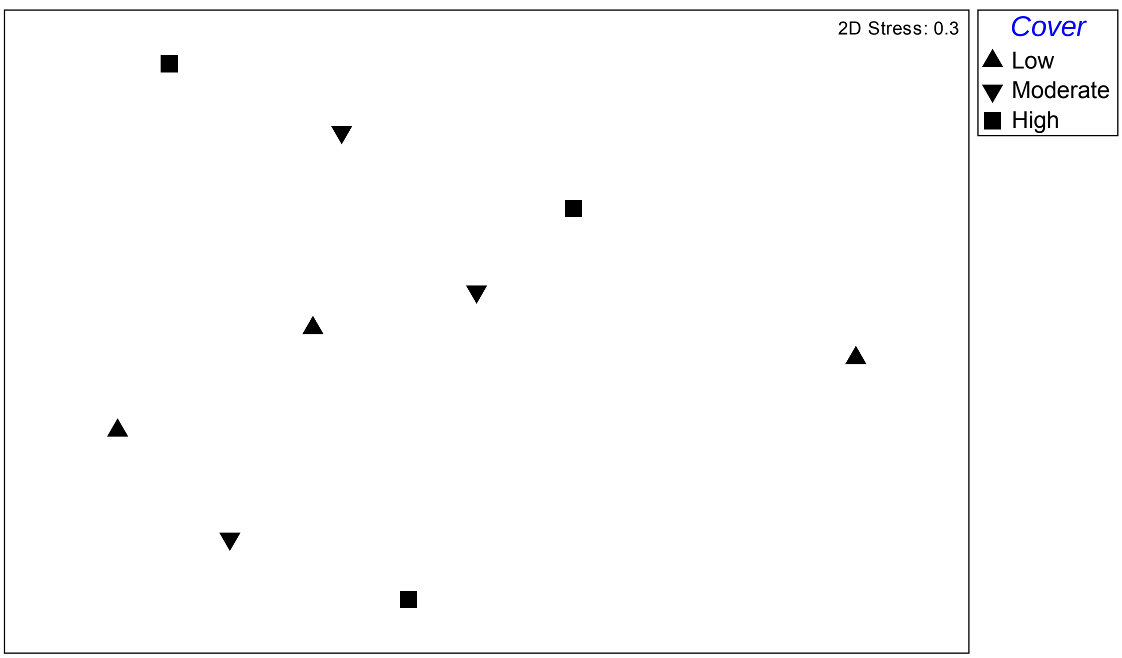

Figure 6.1. The nMDS plot of the data of the 21 most frequently occurring epiphytic macroinvertebrates on *Lagarosiphon* at three levels of vegetation density.

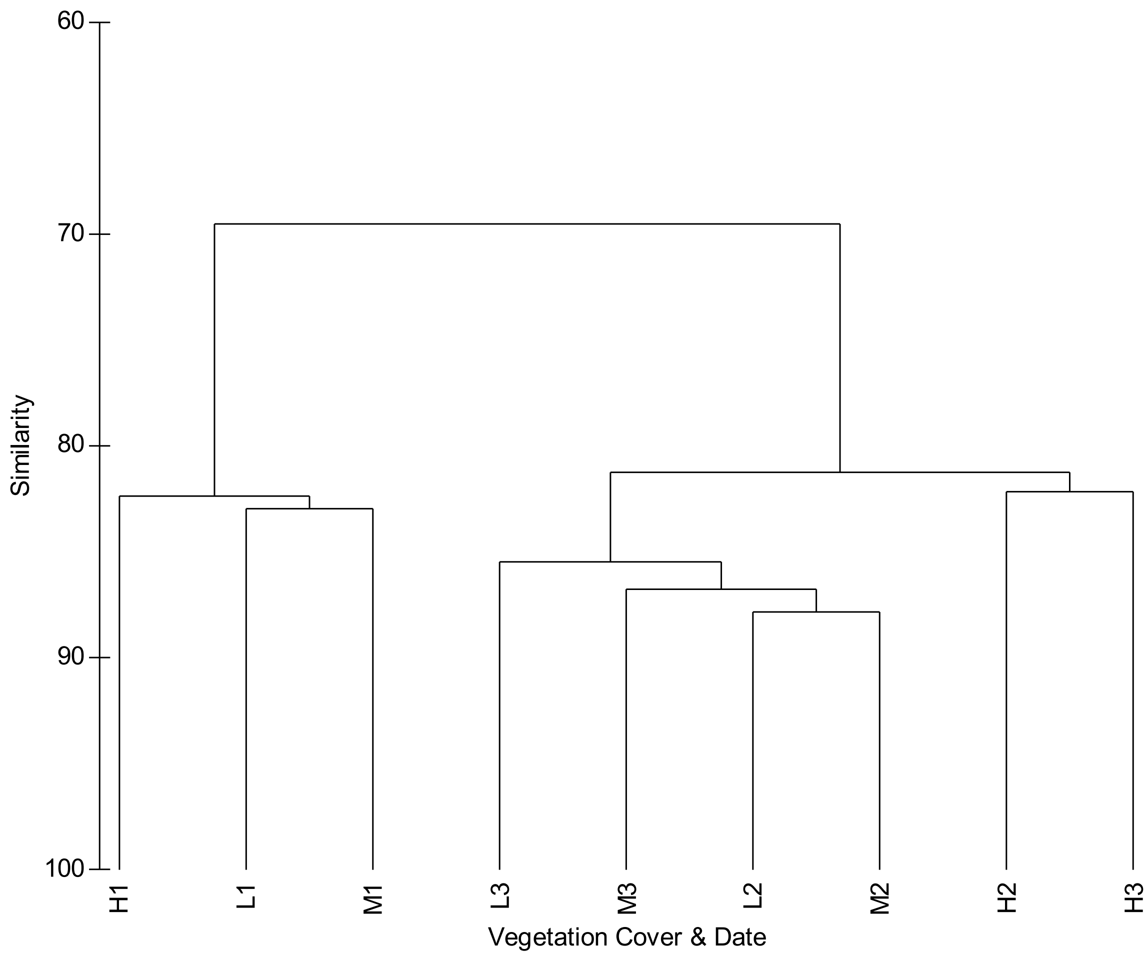

Figure 6.2. Hierarchical clustering showing the Bray-Curtis similarity of epiphytic macroinvertebrates associated with *Lagarosiphon* **at three levels of vegetation density. L, M, & H represents low-, moderate- and high density beds respectively, while (1) represents the first, (2) the second and (3) the third week of sampling.**

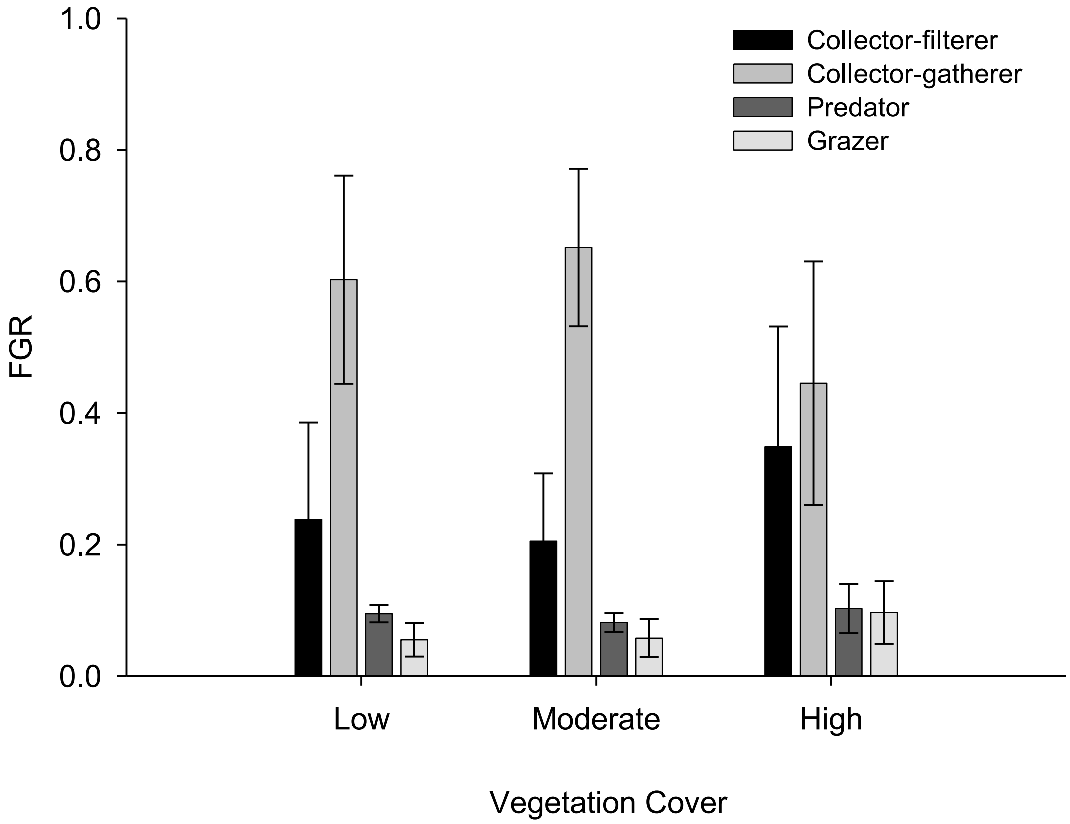

Figure 6.3. Mean (±SE) values of functional group ratios (FGR) from low (L), moderate (M) and high (H) density beds of *Lagarosiphon*

6.3.5 Variation in size structure of *Cloeon* and the Coenagrionidae with vegetation density

In analysing the body size class distribution of the baetid mayfly, *Cloeon*, the specimens were separated into four size categories or classes (SC). The first size category/class (SC1) consisted of insects with total body length of less than or equal to 2mm (TL ≤ 2mm), while SC2 insects had a body length greater than 2 but less than or equal to 4 mm (2 < TL ≤ 4 mm), SC3 were greater than 4 mm but less than or equal to 6 mm (4 < TL ≤ 6 mm) and SC4 had a total body length greater than 6mm (TL > 6 mm).

The largest *Cloeon* size class SC4, was absent in *Lagarosiphon* beds of low density (Figure 6.4). The proportional abundances of insects within SC2 and SC4 were significantly greater than of the smallest of size class (SC1) in low vegetation density beds (Kolmogorov-Smirnov test, p < 0.05). In moderate vegetation density beds the proportion of SC1 was significantly less than those SC2 and SC3, but greater than SC4 (Kolmogorov-Smirnov test, p < 0.05). In high density beds the proportions of SC1, SC2 and SC3 were not significantly different (Kolmogorov-Smirnov test, p > 0.05), but all were significantly more abundant than those of SC4 (Kolmogorov-Smirnov test, p < 0.05).

The high-density beds had a significantly greater proportion of the smallest size class (SC1) compared to low and moderate density beds (Kolmogorov-Smirnov test, p < 0.05). There was no significance difference in the percent proportions of SC2 and SC3 among all three density categories (Kolmogorov-Smirnov test, p > 0.05). While absent from low-density beds, the largest size class (SC4) was present in low numbers in moderate and high density beds, but with no significant difference in percent proportions between the two categories (Kolmogorov-Smirnov, p > 0.05).

The size class spectrum of Coenagrionidae naiads that occurred on different density beds of *Lagarosiphon* is shown in Figure 6.5. The analysis was done by separating the organism into five size classes. Size class 1 (SC1) consisted of individuals with total body length less than or equal to 4mm (TL ≤ 4mm), SC2 (4 < TL ≤ 8mm), SC3, (8 < TL ≤ 12mm), SC4 (12 < TL ≤ 16) and SC5 (TL > 16mm).

The Coenagrionidae were dominated by small-sized individuals, which contributed on average more than 50% in low and moderate-density beds and just over 40% in high-density beds (Figure 6.5). In low and moderate-density beds the proportional abundance of SC1 was significantly greater than of all other size classes (Kolmogorov-Smirnov test, p < 0.05), while that of SC2 was significantly greater than SC5. The largest size class (SC5) did not occur in high-density beds, but was present in low proportions in the low and moderate-density beds. There was no significant difference in proportions of the first four size classes of coenagrionid naiads among the three vegetation density beds (Kolmogorov-Smirnov test, $p < 0.05$).

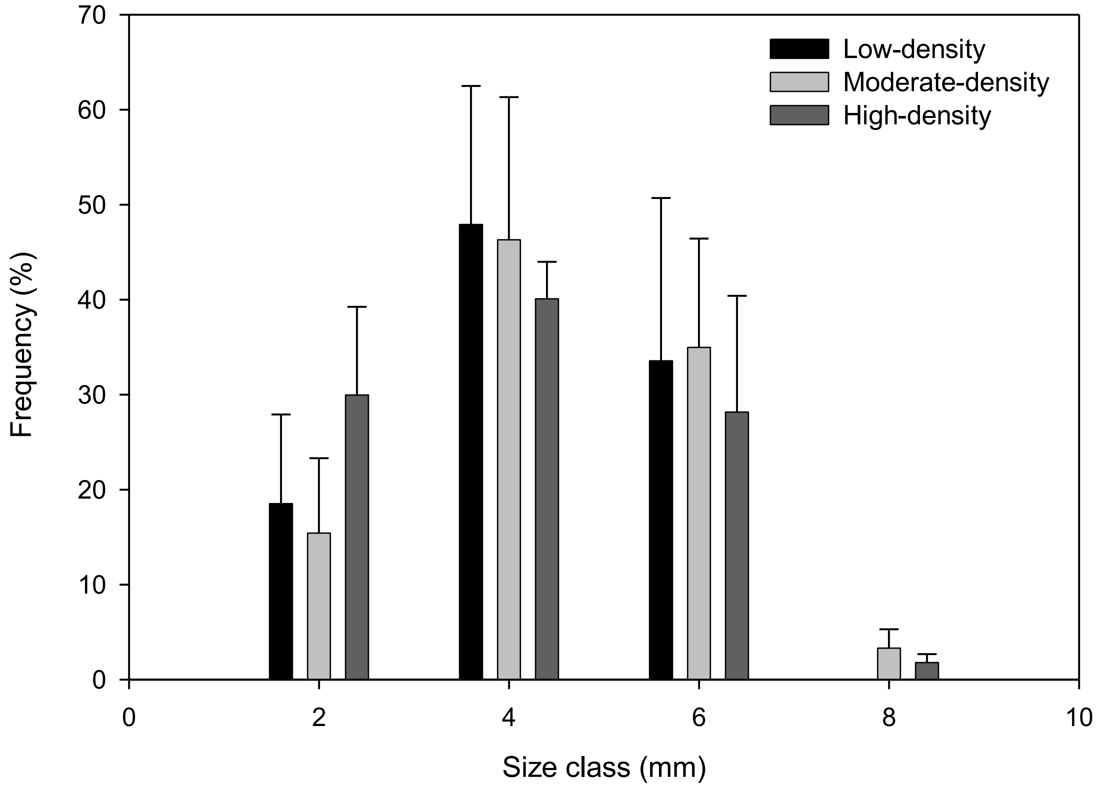

Figure 6.4. Body size frequency distribution of *Cloeon* that occurred in low, moderate and high-density beds of *Lagarosiphon*. It is important to note that the results may be a sampling artefact reflecting the small numbers of these animals that were present in all of the density beds.

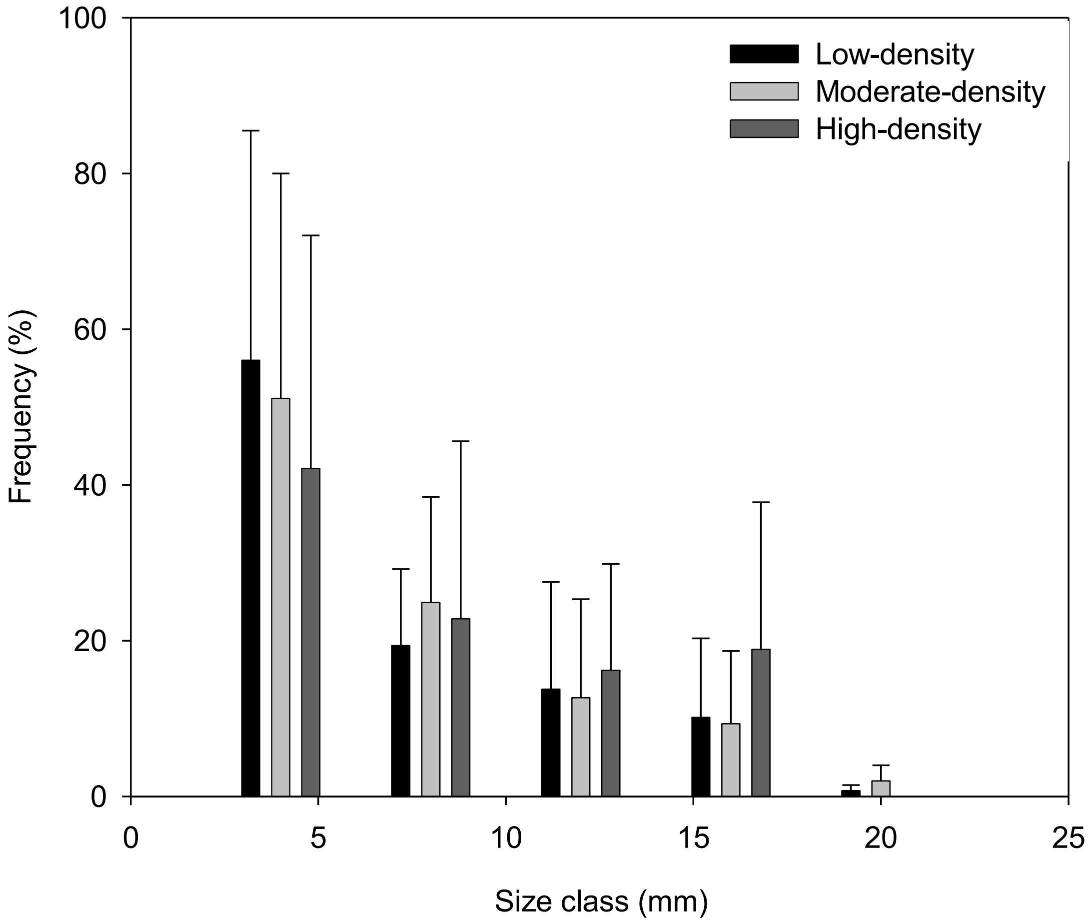

Figure 6.5. Body size frequency distribution of Coenagrionidae naiads that occurred in low, moderate and high density beds of *Lagarosiphon*. **It is important to note that the results may be a sampling artefact reflecting the small numbers of these animals that were present in all of the density beds.**

6.4 Discussion

A number of studies have shown that macrophyte density is an important factor in structuring macroinvertebrate communities, and affects macroinvertebrate abundance, composition and diversity (e.g., Tolonen *et al.* 2003, 2005, Strayer & Malcom 2007).

The current study was carried out to assess whether the epiphytic macroinvertebrate assemblage associated with *Lagarosiphon* in shallow marginal waters of Lake Kariba conforms to the general trends in abundance and diversity with change in vegetation density. It was initially expected, based on the hypothesis that fish predation has a greater impact in simple habitats, that differences in the density of beds of *Lagarosiphon* would result in differences in macroinvertebrate abundance, richness and diversity. Generally, in lakes with fish, the invertebrate abundance and habitat complexity are normally directly correlated (Cyr & Downing 1988a, Zimmer *et al.* 2000). The results of my study did not conform to the original expectations. The macroinvertebrate community composition, abundance and diversity from low, moderate and high-density monospecific beds of *Lagarosiphon* were not different. Physicochemical conditions within beds of different vegetation density were also generally similar during the study period.

Many epiphytic invertebrates tend to be algivores (Dvorak & Best 1982). The macroinvertebrate assemblage associated with *Lagarosiphon* in all three vegetation density categories was dominated by collector-gatherers and filterers, mainly ostracods, chironomids and the conchonstracan *C. hislopi*. Ostracods are generally scavengers and detritus feeders, although there are some species that graze on algae, mostly diatoms on littoral macrophytes (Martens 2001). Most chironomid larvae feed on algae or detritus on submerged substratum (Harrison 2003), while *C. hislopi* is an algal and detritus filter feeder (Belk 1982, Martin 1989). Some studies have shown a decrease in proportions of filterers with increase in macrophyte density (e.g., Rennie & Jackson 2005), which has been attributed to decline in suspended algal levels in dense macrophyte beds due to shading and reduction of water currents, with concomitant sedimentation of algae and other organic particles (Carpenter & Lodge 1986, Hamilton *et al*. 1990). The consistently high abundance of collector gatherers and filterers across the three levels of macrophyte density suggests that steady and unvarying quantities of food in the form of detritus and algae, was available for these feeding groups on *Lagarosiphon* during the sampling period.

Fish predation plays an important role in structuring invertebrate community structure in aquatic systems (Wahlström *et al.* 2000, Rettig 2003, Rennie & Jackson 2005). The predation hypothesis suggests that in complex habitats, such as those associated with dense macrophyte beds, the impacts of fish predation on macroinvertebrate abundance, diversity and body size are greatly reduced (Gilinsky 1984, Diehl & Eklöv 1995, Tolonen *et al.* 2003). In the current study there were no discernable patterns in overall macroinvertebrate abundance, assemblage composition and diversity with variation in density of *Lagarosiphon*. Fish predators tend to be size-selective, preying mainly on large and easily detectable prey (Wellborn *et al.* 1996). The overall dominance of small-bodied taxa, such as Ostracods, *C. hislopi*, Chironominae and Oligocheata, in all three vegetation density categories suggests uniformly high fish predation impact irrespective of vegetation density. According to Tolonen *et al*. (2003) small body size is a characteristic feature among prey species subject to high fish predation. This infers that fish predation had uniform impact on macroinvertebrate abundances, richness and diversity across the *Lagarosiphon* density spectrum.

Overall, there were few large invertebrate predators associated with *Lagarosiphon* in all three vegetation density categories. The low abundance of medium- to large-bodied invertebrate predators and dominance of small-sized invertebrate taxa in freshwater bodies with fish predators is generally attributed to size-selective fish predation (Morin 1984a, b, Tate & Hershey 2003). This further supports the suggestion that the impact fish predation was relatively uniform across the vegetation density gradient, contrary to findings by a substantial number of studies (e.g., Crowder & Cooper 1982, Gilinsky 1984, Diehl 1992, 1995, Zimmer *et al.* 2000, 2001, Tolonen *et al.* 2001, Rennie & Jackson 2005). In this study fish density was not assessed, but Vinebrooke *et al.* (2001) found that at high densities omnivorous minnows had great impact on macroinvertebrate communities even in highly complex habitats. Fish in shallow marginal waters of Lake Kariba are generally quite abundant, especially among vegetation beds (per. obs.). Juvenile fish and small-sized fish species probably preferred moderate and high density *Lagarosiphon* beds to avoid being preyed upon by bigger predatory fish and have access to the greater supply of invertebrate prey. Another possible explanation therefore for the similarities in macroinvertebrate community structure among the different density beds of *Lagarosiphon* is that the greater fish densities that probably occurred in moderate- and high-density beds had similar impacts on macroinvertebrates as fewer fish numbers in the low density beds.

The results of body size distribution of the baetid, *Cloeon* suggests possible conformity to the predictions of the predation hypothesis. *Cloeon* is prey for both fish and macroinvertebrate predators. Coenagrionidae are the most abundant large predatory macroinvertebrate taxa associated with *Lagarosiphon* that prey on *Cloeon* (see also Chapters 3 and 4). As mentioned earlier fish predators prefer large and easily detectable prey. Thus, the largest individuals of *Cloeon* were collected from moderate and high density, and none occurred in low density beds of *Lagarosiphon*, probably as a result of predator avoidance by large individuals or the extermination of large individuals from sparse low density beds by invertebrate and fish predators.

Of interest was that large-bodied individuals of Coenagrionidae were absent from high density beds but were present in low and moderate vegetation density beds. I initially expected that the largest Coenagrionidae in terms of body size would largely be confined to high vegetation density beds in order to avoid predation by fish. Coenagrionid naiads are predators whose prey includes a range of smaller invertebrate taxa. Their presence in low and moderate density beds and apparent avoidance of high density beds may be because predation success is higher in low to moderate density compared to high density beds. The high density macrophyte beds increase habitat complexity, which provide prey more opportunities to escape predation by increasing the availability of hiding places or reducing predator foraging activities (Gilinsky 1984, Hixon & Menge 1991).

6.5 Conclusion

This study shows that contrary to initial expectations there was no distinctive variation in overall and individual macroinvertebrate taxon abundance, composition, richness and diversity associated with varying densities of *Lagarosiphon* in Lake Kariba. The hypotheses that increase in vegetation density results in increases in abundance and diversity of the macroinvertebrate community could not be supported. Although fish abundances were not measured in this study the results suggests that fish predation had the same impacts in low, moderate and high density beds, especially with respect to macroinvertebrate taxa composition, richness and diversity. The size class distribution of *Cloeon* did conform to the prediction of the predation hypothesis, as large-bodied individuals were absent from low- and moderated-density beds, but present in high-density beds. The size-class distribution of coenagrionid naiads in which large-sized individuals occurred in low- and moderate-density beds, but not in high density bed was probably the result of greater foraging success in low to moderate density compared to high-density beds or an effect of greater fish predation intensity in high-density beds compared to low and moderate bed. Further experiments are needed to verify whether these results are consistent over a longer temporal and broader spatial scale on Lake Kariba.

Fish are generally the top predators in freshwater habitats and tend to greatly affect invertebrate assemblages. Invertebrate predation may also have a profound effect on invertebrate assemblages especially in fishless habitats (e.g., Morin 1984a, b, Åbjörnsson *et al.* 2004). In Chapter 7 I assessed the insect assemblage structure that colonised fishless ponds in which *Lagarosiphon* and *Vallisneria* were cultured. The study explored the effect of habitat complexity on insect assemblage as well as on predator-prey interactions among insects in the absence of fish predation.

CHAPTER 7

AQUATIC INSECTS ASSOCIATED WITH *Lagarosiphon* and *Vallisneria* IN FISHLESS PONDS

7.1 Introduction

The structure, composition and trophic interactions of aquatic invertebrate communities are affected not only by habitat complexity but also by the presence or absence of predatory fish (Diehl 1992, Batzer *et al.* 2000, Zimmer *et al.* 2001). Fish predation has strong effects on invertebrate community structure (Morin 1984a, b, Diehl 1992, Nyström *et al*. 2001, Åbjörnsson *et al*. 2002). Fish predators are size-selective and so large-bodied invertebrates, particularly predatory taxa, tend to be more adversely affected than small-bodied taxa (Morin 1984a, b, Wellborn *et al*. 1996). In fishless freshwater habitats medium- to large-sized predatory invertebrate taxa generally dominate the invertebrate assemblage, replacing fish as the main predators (Wissinger & McGrady 1993), and strongly affect the abundances of small non-predatory invertebrates (McPeek 1990, Nyström & Åbjornsson 2000, Åbjornsson *et al*. 2002). Invertebrate taxa that usually occur in fish-free waters are usually more active and grow much faster than those in waters with fish (Steiner *et al.* 2000). In aquatic environments with or without fish predators, differences in habitat complexity should result in differences in macroinvertebrate community structure, composition and diversity.

The two most common and abundant submerged macrophytes in Lake Kariba, *Lagarosiphon ilicifolius* and *Vallisneria aethiopica* are morphological different. *Vallisneria* has basal rosettes of flexible ribbonlike leaves that can occupy the full height of the water column in shallow waters. *Lagarosiphon,* which also can occupy the full height of the water column in shallow waters, has filiform stems that are circular in transverse section, with small sessile and mostly alternate leaves. Thus morphologically, *Lagarosiphon* is more complex than *Vallisneria*. Both plants can occur in extensive monospecific underwater meadows. In Chapter 3, I assessed macroinvertebrates on *Lagarosiphon* and *Vallisneria* in Lake Kariba and found that the same macroinvertebrate taxa occur on both plants. I also found that most of the taxa were much more abundant on *Lagarosiphon* than on *Vallisneria*. These results were attributed to greater refuge from fish predation and possibly greater quantities of food availed by *Lagarosiphon* compared to *Vallisneria.*

In this study I set out to determine whether the aquatic insect assemblage associated with the two plants differs in fishless ponds. The hypothesis tested was that differences in morphological complexity between the two plant species would result in the establishment or colonization by different insect assemblages. Generally, habitat complexity has positive influence on abundance and taxonomic richness of animals in both terrestrial and aquatic environments (Bell *et al.* 1991). I therefore expected that a more diverse and more abundant insect assemblage would be established on *Lagarosiphon* than on *Vallisneria* in fishless ponds. I also explored the effect of habitat complexity on predator-prey interactions among insect taxa.

7.2 Materials and Methods

This study was carried in six small circular ponds (diameter 2.2 m and depth range 0.7 – 0.9 m). *Lagarosiphon* was cultivated in two ponds (Ponds 2 and 3) and *Vallisneria* in another two ponds (Ponds 1 & 4). The remaining two ponds were cultured with both plants in which the ponds were divided into half, with one side cultivated with *Lagarosiphon* and the other with *Vallisneria*. The plants were cultivated in August/September 2007 and sampling for aquatic insects from the ponds was done every fortnight over a period of six weeks in July – August 2008. A detailed description of the materials and methods used in this study is presented in section 2.3.5.

7.3 Results

7.3.1 Water quality in ponds

The variation in selected water parameters in the six ponds during the six-week study period are shown in Figure 7.1. The mean values of the parameters are shown in Table 7.1. Relatively, higher average conductivity values were recorded in Ponds 1 and 4, in which *Vallisneria* was the only plant, than in the other four ponds (Table 7.1). Principal component analysis (PCA) showed that the first and second axes accounted for 49.7% and 26.4 % of the variation in water physicochemical aspects of the ponds (Table 7.2). The first axes was largely correlated with pH and conductivity, while the variation in the second axes was largely due to temperature differences (Table 7.2). Comparatively, the third and fourth axes were unimportant and accounted for 17.2% and 6.7% respectively of the variation in water physicochemical conditions.

PCA clearly separated Pond 1 from the other five ponds, with the separation largely occurring along the first axes (Figure 7.2). Cluster analysis also showed that Pond 1 was distinctly different from the other ponds with respect to water physicochemical attributes (Figure 7.3). The other five ponds were separated into two groups, with Ponds 2, 3 and 4 comprising one group, and Ponds 5 and 6 making up the other group (Figure 7.3). Thus, water physicochemical conditions were quite similar in the ponds that had both *Lagarosiphon* and *Vallisneria* (Ponds 5 & 6). Similarity was also relatively high in the two ponds in which *Lagarosiphon* was the only plant (Ponds 2 & 3). The water physicochemical characteristics of Pond 4, in which *Vallisneria* was the only plant, were similar to those in Ponds 2 & 3 (Figure 7.3).

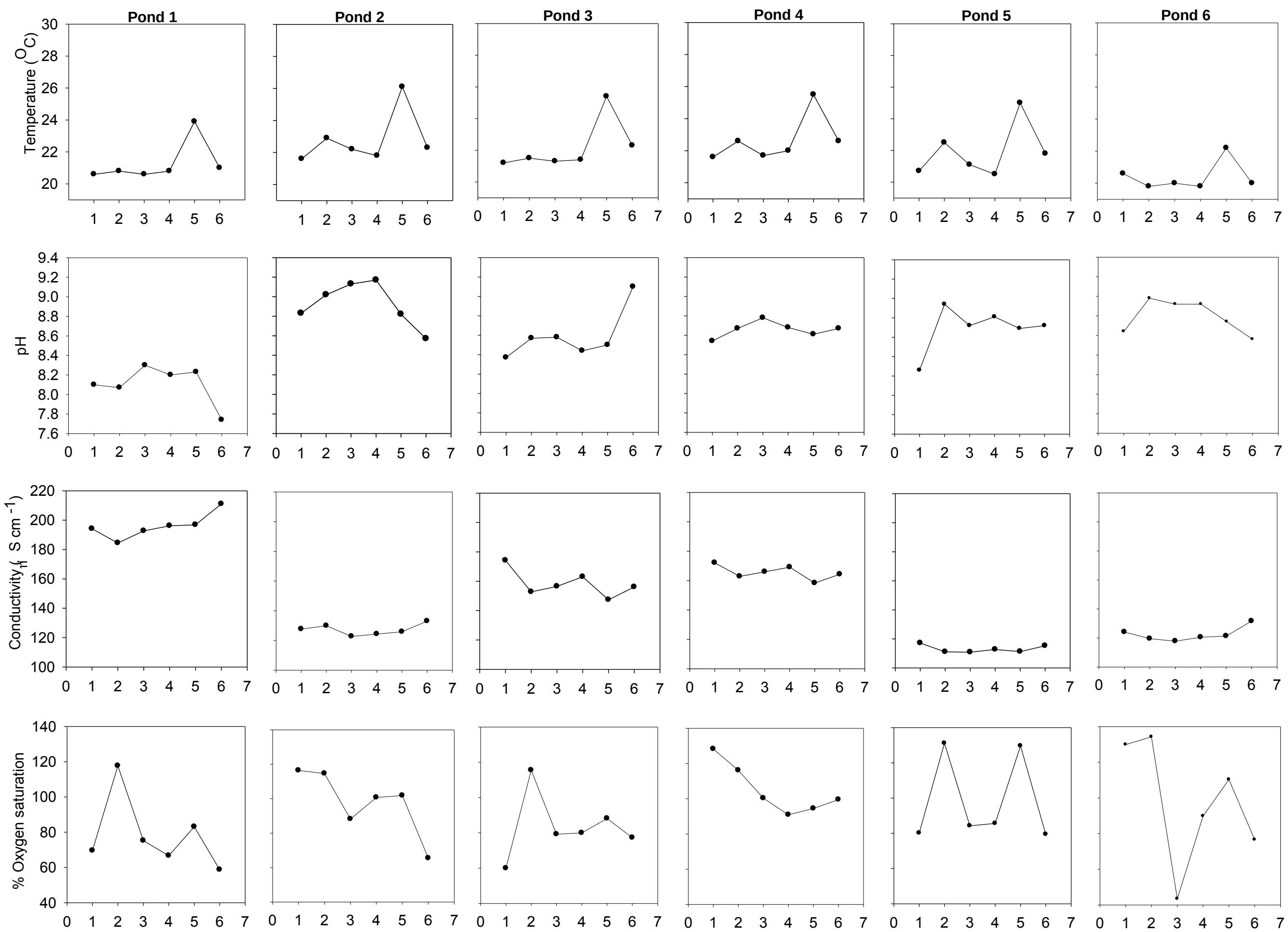

Figure 7.1. Variation in selected water parameters in the ponds during the six-week sampling period.

Table 7.1. Mean (±SE) values of selected water parameters in the six experimental ponds during the study period.

Pond	Vegetation	Temperature (^{O}C)	pH	Conductivity (μScm^{-1})	Oxygen (%sat)
1	*Vallisneria*	21.3 ± 0.5	8.1 ± 0.1	195.9 ± 3.5	78.5 ± 8.5
4	*Vallisneria*	22.7 ± 0.6	8.7 ± 0.0	165.4 ± 2.0	104.9 ± 5.9
2	*Lagarosiphon*	22.8 ± 0.7	8.9 ± 0.1	127.2 ± 1.5	97.9 ± 7.7
3	*Lagarosiphon*	22.2 ± 0.7	8.6 ± 0.1	158.3 ± 3.8	83.3 ± 7.5
5	*Lagarosiphon*/*Vallisneria*	21.9 ± 0.9	8.7 ± 0.1	113.0 ± 1.1	98.3 ± 10.2
6	*Lagarosiphon*/*Vallisneria*	20.4 ± 0.4	8.8 ± 0.1	122.5 ± 2.0	97.4 ± 14.1

Table 7.2. Factor loading of water physicochemical parameters in PCA.

	PC1	PC2	PC3	PC4
Temperature	0.203	-0.844	-0.490	0.081
pH	0.625	0.216	-0.232	-0.713
Conductivity	-0.605	-0.330	0.203	-0.696
Oxygen	0.449	-0.363	0.816	0.019
Eigenvalue	1.99	1.05	0.69	0.27
% Variation explained	49.7	26.4	17.2	6.7

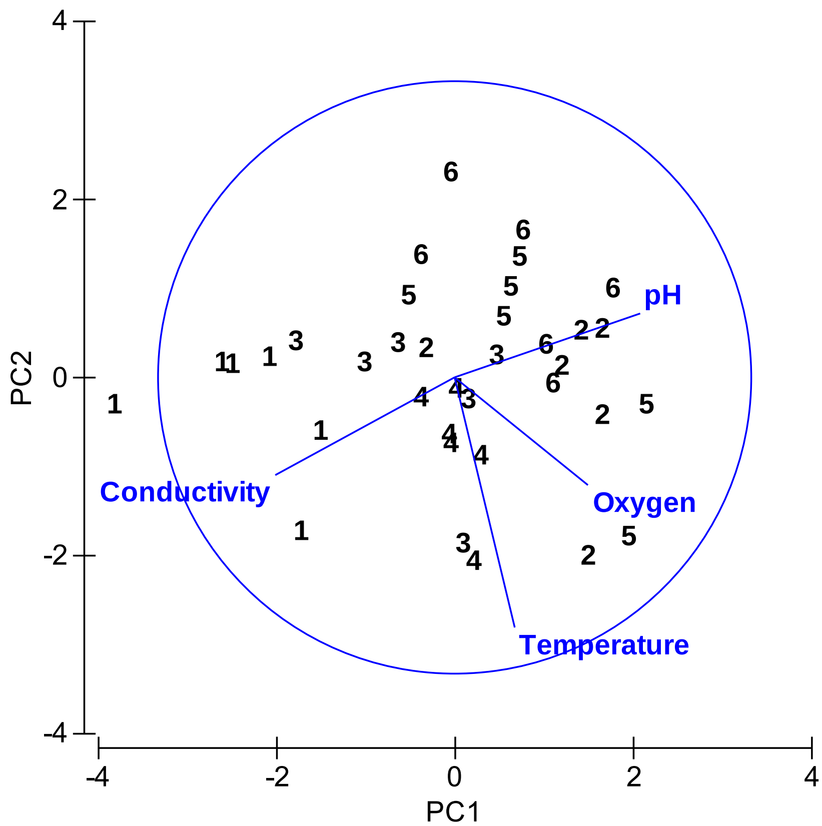

Figure 7.2. PCA plot of water physiochemical attributes of the ponds. The numbers 1 to 6 represents the six ponds. During the sampling period six measurements of water physicochemical aspects were obtained from each pond.

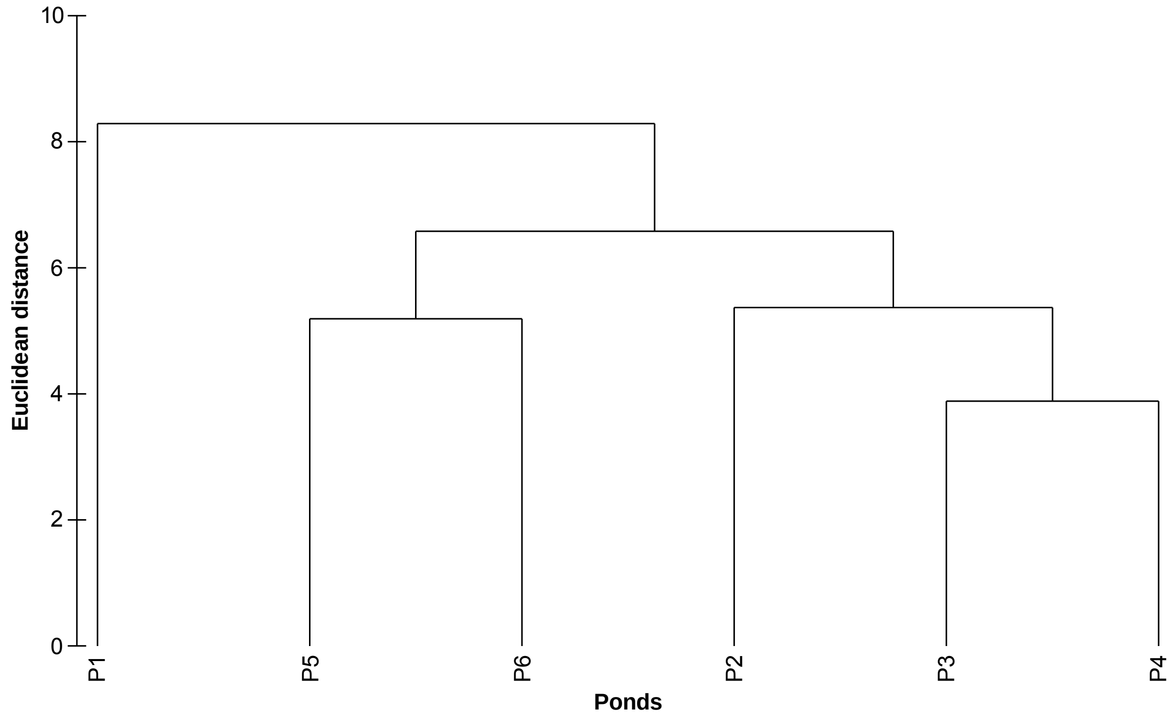

Figure 7.3. Results of cluster analysis based on water physicochemical parameters of the ponds. Euclidean distance as a similarity measure and the group average as a linkage method were used.

7.3.2 Insect assemblage structure associated with *Lagarosiphon* and *Vallisneria*

A total of 970 insects comprising sixteen taxa, eleven of which were predators, were collected during the study. Overall, 3 and 5 taxa were collected from Ponds 1 and 4, compared to 7 taxa from Ponds 3 and 6, and 10 taxa from Ponds 2 and 5 (Table 7.3). Thus, the average number of taxa per sweep tended to be lower in the ponds in which *Vallisneria* was the only plant (Table 7.3). The average total insect abundance was much lower in Ponds 1, 4 and 6, compared to Ponds 2, 3 and 5, whilst diversity was also greatly reduced in Ponds 1, 4 and 5 compared to Ponds 2, 3 and 6 (Table 7.3). Thus, compared to the ponds that had been cultured with *Lagarosiphon* either alone or together with *Vallisneria*, the overall number of taxa, and mean insect abundance and diversity were generally much lower in ponds cultured solely with *Vallisneria*.

A comparison of insect assemblages associated with *Lagarosiphon* (Ponds 2 and 3) and *Vallisneria* (Ponds 1 and 4) growing in separate ponds (Table 7.4) showed that taxa richness (total number of taxa and mean number of taxa per sweep), total insect abundance and diversity were all much greater on *Lagarosiphon* than on *Vallisneria*. The average number of taxa, insect abundance and diversity on *Vallisneria* from ponds in which it was the only plant were all greatly reduced than on *Vallisneria* when grown alongside *Lagarosiphon* or when compared to *Lagarosiphon* growing either singly or in mixed ponds (Table 7.4). Thus the least number of insect taxa, and lowest diversity and insect abundance, were associated with *Vallisneria* when it grew as the only plant in the ponds (Table 7.4).

Table 7.3. Insect assemblage metrics (±SE) recorded in the six experimental ponds during the study period. V and L denote *Vallisneria* and *Lagarosiphon*, while VL indicates the presence of both plant species in the ponds.

	Pond 1 V	Pond 4 V	Pond 2 L	Pond 3 L	Pond 5 VL	Pond 6 VL
Total no. of taxa	3	5	10	7	10	7
Number of taxa/sweep	2.0 ± 0.0	3.0 ± 0.6	5.7 ± 0.7	5.3 ± 0.3	5.7 ± 0.3	4.0 ± 0.5
Total abundance/sweep	8.2 ± 2.5	9.1 ± 2.2	26.8 ± 6.3	18.1 ± 5.1	41.8 ± 8.8	10.2 ± 1.4
Diversity (Shannon H' index)	0.60 ± 0.04	0.79 ± 0.17	1.20 ± 0.04	1.31 ± 0.12	0.88 ± 0.06	1.07 ± 0.09

Table 7.4. Insect composition and abundances (no. per sweep) on *Vallisneria* and *Lagarosiphon*, from ponds in which the plants were cultured as single monospecific stands and ponds in which both plants occurred alongside each other in two separate stands. The total and mean number of taxa, overall mean abundance and macroinvertebrate diversity on each plant species are also shown.

	Vallisneria (Ponds 1 & 4) (n = 6)	*Lagarosiphon* (Ponds 2 & 3) (n=6)	*Vallisneria* (mixed) (Ponds 5 & 6) (n=6)	*Lagarosiphon* (mixed) (Ponds 5 & 6) (n=6)
Cloeon		1.1 ± 0.4	0.1 ± 0.1	0.2 ± 0.2
Enallagma		0.1 ± 0.1	0.4 ± 0.3	0.3 ± 0.2
Ischnura				0.2 ± 0.2
Hemicordulia		8.1 ± 2.6	6.8 ± 2.6	18.4 ± 1.0
Tramea			0.3 ± 0.2	0.4 ± 0.2
Diplacodes		6.1 ± 1.7	6.6 ± 3.1	12.2 ± 6.1
Trithemis	5.9 ± 1.1	3.4 ± 1.9	1.9 ± 0.7	2.8 ± 0.3
Mesovelia		0.1 ± 0.1		
Micronecta	0.1 ± 0.1	0.2 ± 0.1		
Anisops	1.5 ± 0.5	2.0 ± 1.0	0.7 ± 0.4	0.2 ± 0.2
Plea		0.2 ± 0.2		
Dysticidae	0.1 ± 0.1	0.1 ± 0.1		0.1 ± 0.1
Chaoborus	0.9 ± 0.6	1.0 ± 0.6	0.1 ± 0.1	
Chironominae		0.2 ± 0.2		
Culex			0.1 ± 0.1	
Tabanidae			0.1 ± 0.1	
Total no. of taxa	5	12	10	9
Mean no. of taxa	2.5 ± 0.3	5.5 ± 0.3	5.0 ± 0.7	4.8 ± 0.4
Insect abundance (no. per sweep)	8.6 ± 1.5	22.4 ± 4.1	17.1 ± 3.8	34.8 ± 11.6
Shannon Diversity (*H′*)	0.70 ± 0.09	1.26 ± 0.06	1.00 ± 0.06	0.95 ± 0.11

Table 7.4 also shows the mean abundances of the different insect taxa. In all six ponds the insect assemblage was dominated by invertebrate predators. Three anisopteran taxa, *Hemicordulia*, *Diplacodes* and T*rithemis*, were especially abundant and comprised 40.2%, 30.0% and 16.9% respectively of the total number of insects collected from the ponds. In ponds that were cultured solely with *Lagarosiphon* (Ponds 2 and 3), twelve taxa were collected and were numerically dominated by *Hemicordulia* (36.2%), *Diplacodes* (27.1%) and *Trithemis* (15.2%). In ponds in which *Lagarosiphon* was grown alongside *Vallisneria* (Ponds 5 and 6), *Hemicordulia* comprised 52.9% of the insects on *Lagarosiphon*, while *Diplacodes* and *Trithemis* made up 35.0% and 16.9% respectively. *Hemicordulia* (40.0%), *Diplacodes* (38.9%) and *Trithemis* (11.1%) were also the major taxa associated with *Vallisneria* in ponds cultured with the two plants. Both *Hemicordulia* and *Diplacodes* were absent from ponds in which *Vallisneria* was the sole plant (Ponds 1 and 4), and *Trithemis* dominated making up 68.7% of the insect assemblage (Table 7.4). In Pond 5, the mean abundances of *Hemicordulia* (32.0 $\pm$ 16.7) and *Diplacodes* (21.7 $\pm$ 9.8) on *Lagarosiphon* were generally greater than on *Vallisneria*, which had average abundances of 9.6 $\pm$ 4.7 and 11.1 $\pm$ 5.1 respectively. The mean abundance of *Trithemis* in Pond 5 was generally similar between *Lagarosiphon* (2.9 $\pm$ 0.5) and *Vallisneria* (1.4 $\pm$ 0.1). In Pond 6 the abundances of the three main anisopteran taxa were generally similar between the two plant species, with the mean abundance of *Hemicordulia*, *Diplacodes* and *Trithemis* on *Lagarosiphon* being 4.7 $\pm$ 2.4, 2.6 $\pm$ 1.0, and 2.7 $\pm$ 0.6 respectively, compared to 4.1 $\pm$ 1.8, 2.2 $\pm$ 0.6 and 2.8 $\pm$ 1.0 respectively, on *Vallisneria*.

Analysis of similarities (ANOSIM) of the insect assemblages (Table 7.5) and the 2D MDS plot (Figure 7.4) showed that the insect assemblage on *Vallisneria* in single-plant ponds was different from that on *Vallisneria* when it grew alongside *Lagarosiphon*. The insect community associated with *Vallisneria* from single plant ponds was also distinctly different from that associated with *Lagarosiphon* when it was the only plant in the pond or when cultured together with *Vallisneria* (Table 7.5). In ponds in which *Vallisneria* was the only plant, similarity in insect assemblage among samples was about 68%, with *Trithemis* overwhelmingly contributing 72%, and *Anisops* 24% to average similarity (Table 7.6). *Hemicordulia, Diplacodes* and *Trithemis* were the most important taxa that contributed to similarity among samples in assemblage structure of insects associated with *Vallisneria* cultured with *Lagarosiphon* and with *Lagarosiphon* in ponds where it was the sole plant or when grown alongside *Vallisneria* (Table 7.6). The high dissimilarity of about 70% of the insect assemblage on *Vallisneria* in ponds where it was the only plant species compared to plants in the other ponds was largely due to differences in the abundances of *Hemicordulia, Diplacodes* and *Trithermis* (Table 7.7).

7.3.3 Size class distribution of dragonfly naiads associated with *Lagarosiphon* and *Vallisneria*

The body length distributions of dragonfly naiads collected from *Lagarosiphon* and *Vallisneria* are shown in Figures 7.5 and 7.6. The frequency distribution of naiad size classes was significantly different when the two plants occurred in separate ponds (Kolmogorov-Smirnov test, D = 0.539, p = 0.013). The size class range of naiads from ponds where *Vallisneria* was the only plant was greatly narrowed compared to that from ponds where *Lagarosiphon* the only plant, and significantly greater numbers of smaller and larger size classes occurred on *Lagarosiphon* than on *Vallisneria* (Kolmogorov-Smirnov test, D = 0.539, p = 0.006) (Figure 7.5). The naiad size-class range associated with *Vallisneria* was from 2.49 to 4.99 mm, and was dominated by one size class (3.00 – 3.49 mm), which was significantly more abundant than all the other size classes (Kolmogorov-Smirnov test, p < 0.05). In ponds that comprised *Lagarosiphon* the size class range was from 0.99 to about 6.99 mm and the body size of most insects falling between 2.00 and 5.00 mm (Figure 7.5).

In ponds where the two plants were cultured together, the size class distribution of dragonfly naiads was similar and there were no significant differences in the proportion of insect size classes from the two plant species (Kolmogorov-Smirnov test, D = 0.188, p = 0.716) (Figure 7.6). The body size of most of the naiads on both plants was between 1.50 and 6.00 mm, with a few naiads greater than 15mm (Figure 7.6).

Table 7.5. Results of pairwise tests following 1-way ANOSIM giving R-statistics and P values for macroinvertebrates associated with *Lagarosiphon* and *Vallisneria* in fishless ponds (R-values range from 0 = pair indistinguishable; to 1 = pair strongly differ).

	Vallisneria		*Lagarosiphon*		*Vallisneria* (mixed)	
	R	P	R	P	R	P
Lagarosiphon	0.883	<0.001				
Vallisneria (mixed)	0.944	<0.001	-0.106	0.797		
Lagarosiphon (mixed)	1	<0.001	0.100	0.212	-0.090	0.714

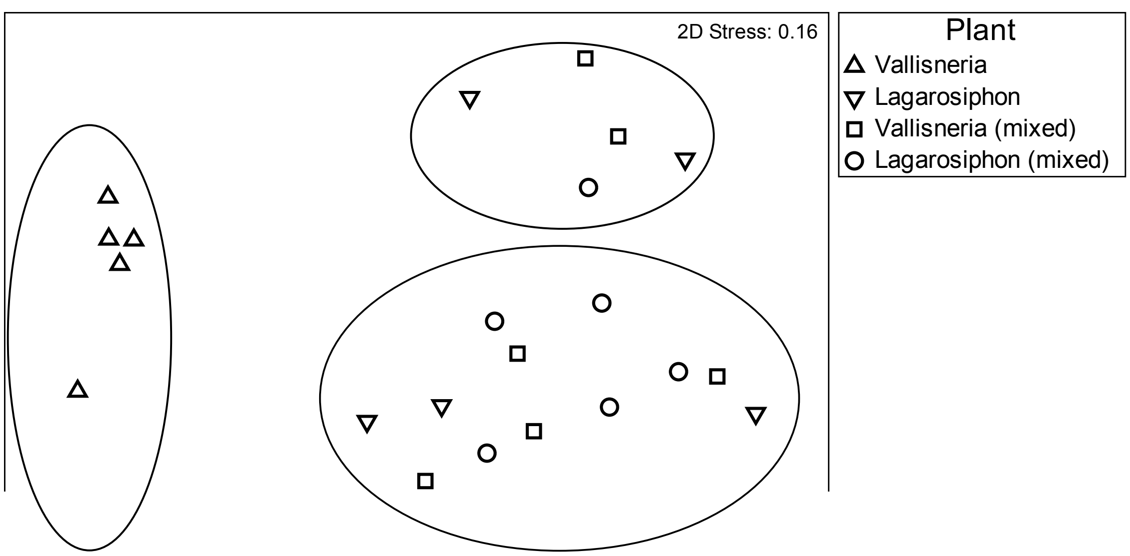

Figure 7.4. MDS 2D ordination of Ln (X + 1) transformed insect taxa abundances associated with *Lagarosiphon* and *Vallisneria* in fishless ponds. *Vallisneria* (mixed) infers that the sample was obtained from *Vallisneria* in ponds where it occurred together with *Lagarosiphon*.

Table 7.6. Results of SIMPER analysis on Ln (X + 1) transformed insect abundance data showing the major taxa contributing to similarity in community structure of insect associated with *Vallisneria* and *Lagarosiphon* in fishless ponds.

Insect Taxa	Vegetation	Similarity Statistics			
		Av. Abund	**Av. Sim**	**Contrib %**	**Cum.%**
	Vallisneria (Av. Similarity = 67.9)				
Trithemis		1.87	48.90	72.00	72.00
Anisops		0.82	16.45	24.22	96.22
	Lagarosiphon (Av. Similarity = 52.7)				
Diplacodes		1.80	20.86	39.59	39.59
Hemicordulia		1.78	13.86	26.30	65.89
Trithermis		1.05	6.34	12.03	77.92
	Vallisneria (mixed) (Av. Similarity = 53.1)				
Diplacodes		1.62	19.65	37.02	37.02
Hemicordulia		1.67	18.7	35.24	72.26
Trithermis		0.92	11.51	21.68	93.94
	Lagarosiphon (mixed) (Av. Similarity = 63.5)				
Hemicordulia		2.32	22.1	34.81	34.81
Diplacodes		2.07	20.27	31.92	66.73
Trithermis		1.32	18.37	28.92	95.65

Table 7.7. Results of SIMPER analysis carried out on Ln (X +1) transformed data showing % contribution to average dissimilarity of insects associated with *Lagarosiphon* and *Vallisneria* in fishless ponds.

Insect Taxa	Comparison	Contribution (%)	Cumulative (%)
	Vallisneria vs. *Lagarosiphon* (Av. dissimilarity = 70.40)		
Diplcaodes		25.93	25.93
Hemicordulia		22.56	48.49
Trithermis		16.17	64.66
Anisops		9.49	74.15
Cloeon		9.13	83.28
	Vallisneria vs. *Vallisneria* (mixed) (Av. dissimilarity = 70.93)		
Hemicordulia		26.59	26.59
Diplacodes		26.28	52.87
Trithermis		15.83	68.70
Anisops		10.72	79.43
	Lagarosiphon vs. *Vallisneria* (mixed) (Av. dissimilarity = 47.12)		
Hemicordulia		20.79	20.79
Diplacodes		16.35	37.14
Trithermis		14.62	51.76
Anisops		13.18	64.94
Cloeon		10.45	75.39
	Vallisneria vs. *Lagarosiphon* (mixed) (Av dissimilarity = 70.83)		
Hemicordulia		31.39	31.39
Diplacodes		28.41	59.80
Anisops		11.37	71.17
Trithermis		8.63	79.80
	Lagarosiphon vs. *Lagarosiphon* (mixed) (Av dissimilarity = 46.33)		
Hemicordulia		22.39	22.39
Diplacodes		15.46	37.85
Trithermis		14.41	52.26
Anisops		13.28	65.54
Cloeon		9.60	75.14
	Vallisneria (mixed) vs. *Lagarosiphon* (mixed) (Av. dissimilarity = 38.82)		
Hemicordulia		28.43	28.43
Diplacodes		24.15	52.58
Trithermis		12.20	64.78
Anisops		8.68	73.47
Tramea		7.16	80.63

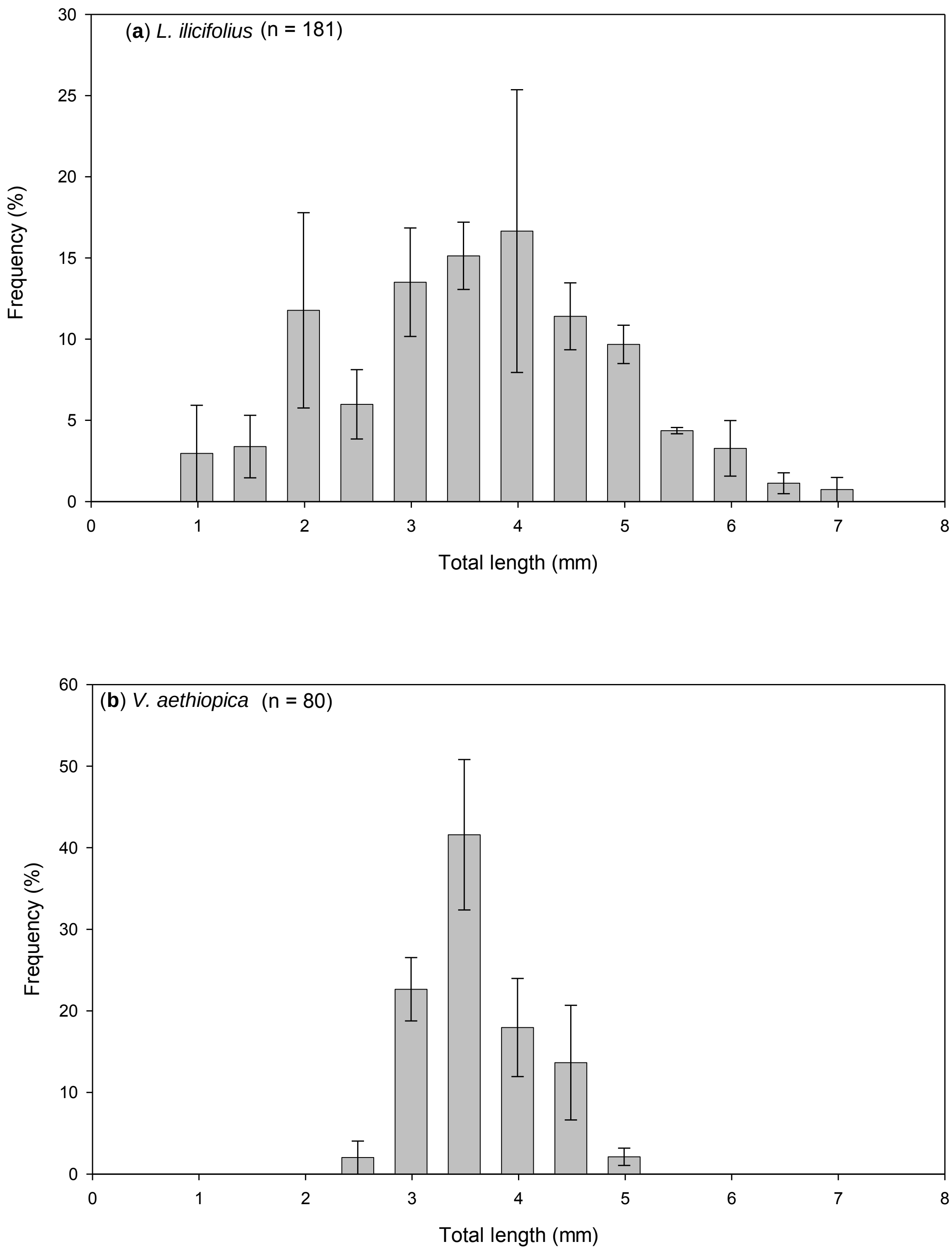

Figure 7.5. Body size distribution of dragonfly nymphs associated with *Lagarosiphon* **and** *Vallisneria* **when the two plant species were cultured in separate ponds.**

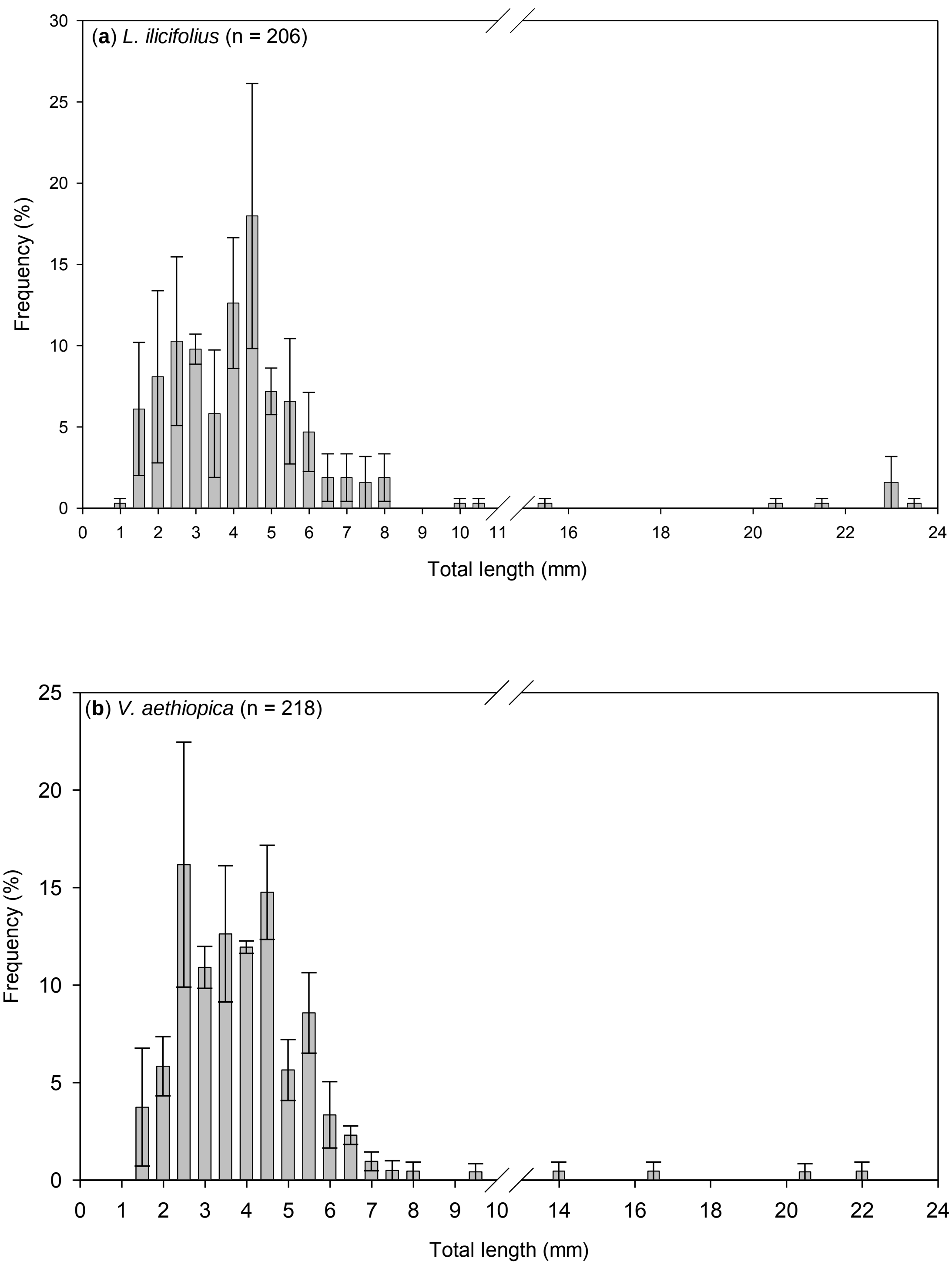

Figure 7.6. Body size class distribution of dragonfly nymphs associated with *Lagarosiphon* and *Vallisneria* from ponds in which the plant were cultured alongside each other.

The total insect abundance, taxa richness, insect diversity and abundances of *Hemicordulia*, *Diplocodes* and *Trithemis* in the ponds were also assessed with respect to the measured water parameters. Total abundance, as well as the abundances of *Hemicordulia* and *Diplacodes* were negatively and significantly correlated with water conductivity, while *Trithermis* was also significantly but positively correlated with conductivity (Spearman Rank correlation, $P < 0.05$) (Table 7.8). This suggests that water quality, in this case conductivity, may have had a role in structuring insect community structure.

Table 7.8. Spearman correlation coefficients (row 1 in each case) and their *p* values (row 2) for the relationship between total insect abundance (number of insects per sweep), taxa richness, insect assemblage diversity, abundances of *Hemicordulia, Diplacodes* **and** *Trithemis* **with water characteristics in the study ponds. Significant correlations are in bold.**

	Temperature	pH	Conductivity	Oxygen
Total insect abundance	0.31	0.60	**-0.83**	0.31
	0.54	0.21	**0.04**	0.54
Taxa Richness	0.41	0.67	-0.78	0.41
	0.43	0.15	0.07	0.42
Diversity	0.31	0.43	-0.43	0.26
	0.54	0.40	0.40	0.62
Hemicordulia	0.23	0.55	**-0.81**	0.20
	0.66	0.26	**0.05**	0.70
Diplacodes	0.23	0.55	**-0.81**	0.20
	0.66	0.26	**0.05**	0.70
Trithemis	0.43	-0.37	**0.89**	0.14
	0.40	0.47	**0.02**	0.79

7.4 Discussion

The aquatic insect assemblage associated with two submerged plant species, *Vallisneria* and *Lagarosiphon*, in fishless ponds was studied. The study shows that the insect assemblage associated with *Vallisneria* when it was the only plant in ponds was markedly different from that associated with *Lagarosiphon* or the assemblage on *Vallisneria* growing in close proximity to *Lagarosiphon*.

7.4.1 Insect assemblage structure on *Lagarosiphon* and *Vallisneria*

The total insect abundance, richness and diversity associated with *Vallisneria* in ponds in which it was the only plant was greatly reduced compared to ponds comprised of *Lagarosiphon*. This agrees with a number of findings (e.g., Kershner & Lodge 1990, Dionne & Folt 1991, Cheruvelil *et al*. 2002), in which total invertebrate abundance and diversity has been shown to differ with change in macrophyte complexity. Most of these previous studies though were conducted in systems in which fish were present and fish predation affected the macroinvertebrate assemblage (e.g., Nyström *et al.* 2001, Äbjörnsson *et al*. 2002, 2004). In the current study the component of fish predation was absent, and differences in macrophyte type and structural complexity as well as interactions among the insects were the main factors structuring insect assemblages on the two plant species.

The findings on insect communities associated with *Vallisneria* and *Lagarosiphon* grown in the same ponds (Pond 5 and 6) were not as conclusive as to the effect of differences in plant morphological complexity on insect community compared to when the plants were grown in separate ponds. When grown together, insect taxa richness and diversity were similar between the two plant species. In one of the ponds (Pond 5) insect abundance on *Lagarosiphon* was significantly greater than on *Vallisneria* while in Pond 6 the total abundance of insects did not differ between the two plants. The similarity in insect composition and diversity when the two plants occurred in the same pond was due to the close proximity of the plants, which enabled movement of insects between plant beds. This implies that in fishless environments morphological differences between *Vallisneria* and *Lagarosiphon* have minimal effects on insect taxa richness, composition and diversity when the two plants grow in close proximity in the same water body, but may affect insect abundances. Jeffries (1993), using artificial pondweeds, also found that an increase in structural complexity was associated with increase in abundance of a number of invertebrate species and total invertebrate abundance. In contrast, Rennie & Jackson (2005), using macrophyte weed bed density as a measure of habitat complexity, found that in fishless lakes increased macrophyte complexity had no effect on invertebrate abundances, but in lakes with fish, invertebrate abundance was positively and strongly associated with macrophyte complexity. In the absence of predatory fish in freshwater bodies, intermediate to large predatory insect taxa tend to dominate the invertebrate assemblage (Wellborn *et al.* 1996).

7.4.2 Habitat complexity, predator-prey interactions and insect assemblage structure

In the present study, the insect community in all ponds was dominated by anisopteran nymphs. *Trithemis* was the dominant taxon and only odonate in ponds cultured with *Vallisneria*. In the other ponds, consisting solely of *Lagarosiphon* or both *Lagarosiphon* and *Vallisneria*, three dragonfly taxa, *Hemicordulia*, *Diplacodes* and *Trithemis* dominated. A fourth anisopteran, *Tramea*, was also collected from both plant species when they were cultured in the same pond. Odonates, mostly dragonfly nymphs, tend to be the main predators in the littoral and shallow water zones of freshwater systems without fish (Wissinger & McGrady 1993, Åbjörnsson *et al.* 2004). The occurrence of one taxon, *Trithemis*, in ponds in which *Vallisneria* was the only plant, suggests greater inter-odonate interactions compared to ponds consisting of *Lagarosiphon* or both plants. The preying of odonates on other odonates, that is, mutual or intraguild predation is a key factor in structuring odonate communities in fishless systems (Benke *et al.* 1982, Merril & Johnson 1984, Robinson & Wellborn 1987). Mutual predation may have resulted in exclusion by

Trithemis of all the other odonate taxa from ponds that were cultured solely with *Vallisneria*. In ponds that had *Lagarosiphon* either cultured alone or together with *Vallisneria*, enhanced habitat complexity enabled the coexistence of at least three dragonfly taxa. According to Hampton (2004), habitat complexity enables coexistence of competing organisms by providing refuges and so reducing intraguild predation. Thus in ponds cultured with *Lagarosiphon*, increased habitat complexity enabled the coexistence of three or four dragonfly taxa, possibly through a reduction in mutual predation.

The suggestion that morphological complexity of *Lagarosiphon* dampened mutual predation among odonates was further supported by the distribution of body sizes of naiads. Large odonates will generally eat small ones (Merril & Johnson 1984). The body size-class distribution of the odonate assemblage, from ponds in which *Vallisneria* was the only plant was characterised by a narrow size class range, largely dominated by individuals of one size class. In ponds with *Lagarosiphon* the body size range of odonates was broader with a number of size classes contributing significant proportions to the odonate community. When the two plants were cultured in the same pond, body size distribution of odonate naiads was similar, supporting the inference that close proximity allowed for movement and exchange of insects between the plant beds. Thus in the simple habitat, which consisted entirely of *Vallisneria*, the high levels of predation on small odonates by larger odonates reduced co-occurrence of large numbers of individuals characterised by differences in body size.

7.4.3 Water quality and insect assemblage structure

The study findings also suggest that aspects of insect assemblage structure may have been influenced by water quality in the ponds. Aquatic plants can alter physical and chemical conditions of water bodies (Petticrew & Kalff 1992, Madsen *et al.* 2001) and macrophyte species differing in growth form and physiological capabilities have been shown to have considerably differing effects on water physicochemistry (e.g., Jaynes & Carpenter 1986, Wigand *et al.* 1997). Conductivity was much higher in ponds in which *Vallisneria* was the only plant than in the other four ponds. This raises the question whether the two plants can differentially alter water physical and chemical properties in a water body.

Water chemistry, together with habitat structure, pond area, and macrophyte species richness, have all been found to affect invertebrate communities in small fishless ponds. In the current study the abundances of *Hemicordulia*, *Diplacodes* and *Trithemis* were strongly correlated with water conductivity. Interestingly, *Hemicordulia* and *Diplacodes* were absent from the ponds cultivated solely with *Vallisneria*, while *Trithemis* was the dominant taxa in these ponds. Numerous adult insects have chemo sensors (Bell & Carde 1984), and according to Åbjörnsson *et al.* (2002) females may use the sensors to sample water for the presence of fish predators before ovipositing. Did *Hemicordulia* and *Diplacodes* avoid ovipositing in the ponds that had *Vallisneria* as the only plant because of their water physicochemical condition, in this case comparatively high conductivity? Although the absolute conductivity values in all six ponds were quite low and probably had no effect on insect assemblage structure, further studies are needed to determine how aquatic insects choose ovipositing sites, especially with respect to differences in water quality.

7.4.4 Conclusion

This study generally supports the hypothesis that macrophyte morphological complexity has an important role in structuring insect communities in fishless environments. It shows that in a fishless water body, the two morphologically different macrophytes, *Vallisneria* and *Lagarosiphon,* when growing in close proximity may be associated with similar insect assemblages, though greater numbers may occur on *Lagarosiphon*. The study suggests that when the two plants occur singly in separate fishless water bodies, different insect assemblages may develop, with *Lagarosiphon* having greater taxa richness, diversity and overall abundance than *Vallisneria*. The study also confirms that in the absence of fish predation, invertebrate predators, largely odonates become the top predators, with more complex habitats (*Lagarosiphon*) supporting more taxa, diversity and abundances of insect predators as well as broader range of size classes of predatory insects than less complex habitats (*Vallisneria*).

The results of this study has important implications for Lake Kariba in which, *Vallisneria* and *Lagarosiphon* are the most common and abundant macrophytes in the littoral zones. Development of extensive meadows comprised entirely of *Vallisneria* may result in the development of macroinvertebrate assemblage characterised by low abundances and thus possibly low biomass. This may then negatively affect fish communities since epiphytic macroinvertebrates constitute an important component of the diet for juveniles of many fish species. In the lake, beds of *Lagarosiphon* should support a greater variety and abundance of insects and other epiphytic macroinvertebrates and thus provide greater abundance of food for fish species compared to *Vallisneria*. Therefore extensive beds of *Lagarosiphon* should result in greater fish productivity than weed beds comprised exclusively of *Vallisneria*.

In Chapter 3 I found that invertebrate assemblage composition on *Lagarosiphon* and *Vallisneria* in shallow waters of Lake Kariba was generally the same although there were much greater abundances of most taxa on *Lagarosiphon* than *Vallisneria*. Generally, increase in habitat complexity reduces the foraging efficiency of fish predators (Nelson & Bonsdorff 1990, Swisher *et al.* 1998). I attributed the differences in invertebrate assemblages on the two plants to differences in their structurally morphology. I suggested that the impact of fish predation on epiphytic invertebrates was greater on *Vallisneria* due to its simpler structurally morphology compared to *Lagarosiphon*. The current chapter shows that even in the absence of fish predators epiphytic insect assemblages may differ between the two plant species, especially when they widely separated. In Chapter 8 I used ponds to experimentally assess the effect of fish predation on invertebrates associated with *Lagarosiphon* and *Vallisneria.*

CHAPTER 8

THE EFFECT OF FISH PREDATION ON MACROINVERTEBRATES ASSOCIATED WITH *Lagarosiphon* and *Vallisneria*: A PILOT STUDY IN SMALL PONDS

8.1 Introduction

Predation is an important factor in structuring communities in freshwater ecosystems (Morin 1984a, b). The level of impact on prey communities depends on the ecological attributes of the predator and prey as well as on environmental factors (Dahl & Greenberg 1998). Habitat complexity is a key environmental attribute that affects predator-prey interactions (Dahl & Greenberg 1998). Increased complexity tends to dampen foraging success and efficiency of predators (Dibble *et al.* 1996, Dahl & Greenberg 1998) and so enabling coexistence of predators and their prey (Power 1992).

In aquatic environments fish are among the top predators. In open pelagic zones of lakes, fish predation usually affects the species composition and size structure of zooplankton communities (Rettig 2003). Size-selective predation on large zooplanktonic organisms generally results in increased abundance of small individuals (Wahlström *et al*. 2000, Rettig 2003). Unlike pelagic zones, sections of the littoral zone of most lakes are usually vegetated, and are more complex habitats and so support greater diversity, numbers and biomass of invertebrates than the pelagic zones (Beckett *et al*. 1992a). The enhanced complexity provided by vegetation in littoral zones affects fish predation efficiency on macroinvertebrates. Dense vegetation generally hampers fish predation (Dibble *et al.* 1996), which therefore tends to be much more severe in low-density vegetation (Rennie & Jackson 2005).

The purpose of this study was to explore the impact of fish predation on macroinvertebrates associated with *Vallisneria* and *Lagarosiphon* in small ponds. I hypothesised that due to differences in morphological complexity between the two plants, the effects of fish predation would be much more pronounced on the macroinvertebrates associated with the simpler plant, *Vallisneria*. Macroinvertebrate communities in ponds that were without fish for more than three months were sampled before and after fish were added to the ponds. The results are discussed with respect to the implications on predator-prey relations of macroinvertebrate communities associated with *Vallisneria* and *Lagarosiphon* in Lake Kariba.

8.2 Materials and Methods

This study was carried out in three circular ponds (dimensions of ponds described in Section 2.3.5). In Pond 1, *Vallisneria* grew as the only plant, and in Pond 2 *Lagarosiphon* was the sole plant. Pond 3 contained the two plants, which were maintained as separate stands in two halves of the pond. The ponds were set up in February 2009, and sampled over a period of nine weeks from June to August 2009. While fishless, the ponds were sampled for invertebrates once every week for three weeks, after which 20 juvenile cichlid fish (size class 4 – 10 cm, fish density 5 m^{-2}) were added to each pond. After fish were added ponds 1 and 2 were sampled once every week for six weeks while Pond 3 was sampled five times. A detailed description of the methods used in the study is provided in section 2.3.6.

8.3 Results

8.3.1 Pond 1 (*Vallisneria*)

In Pond 1, which contained *Vallisneria*, the macroinvertebrate community before fish were added was largely comprised of Libellulidae (13.1%), Notonectidae (4.5%), Dytiscidae (17.0%), Chironominae (48.2%) and Tanypodinae (12.0%) (Table 8.1), which altogether comprised 94.9% of the total number of organisms collected from the pond.

After fish were added to Pond 1, numbers of libellulid naiads, notonectids, dytiscids, chironomines and tanypods decreased markedly (Table 8.1). Although Chironominae and Tanypodinae made up 52.5% and 11.2% respectively of the total number of organisms collected after adding fish their abundances were reduced by 70.9% and

75.4% respectively (Table 8.1). The average percent abundances of Libellulidae, Notonectidae and Dytiscidae decreased by more than 95% after fish were added (Table 8.1). The abundances of three taxa, Oligochaeta, Glossiphonidae and Hydracarina increased in the presence of fish, with the abundances of oligochaetes and glossiphonids increasing by 333% and 187% respectively, while water mites were absent before adding fish (Table 8.1).

Before fish were added ten macroinvertebrate taxa comprising Planariidae, Oligochaeta, Hydracarina, Baetidae, Libellulidae, Notonectidae, Dytiscidae, Chaoboridae, Chironominae and Tanypodinae were collected from Pond 1. After fish were added ten taxa, Planariidae, Oligochaeta, Glossiphonidae, Hydracarina, Libellulidae, Notonectidae, Dytiscidae, Chaoboridae, Chironominae and Tanypodinae were collected, although by the sixth week of adding fish only three taxa, Oligochaeta, Glossiphonidae and Chironominae were obtained in small numbers (Table 8.1). The overall mean macroinvertebrate abundance associated with *Vallisneria* in Pond 1 after introducing fish predators (8.43 $\pm$ 2.57) was markedly less than when the pond was fishless (35.08 $\pm$ 10.21). Thus the net effect of adding fish in Pond 1 was a 76.0% reduction in macroinvertebrate abundance associated with *Vallisneria*.

Figure 8.1 shows the size-class distribution of libellulid naiads that were associated with *Vallisneria* in Pond 1. Before fish were introduced a broad range of size classes was present. Libellulid naiads were present up to the third week after fish were introduced and completely absent in the samples thereafter. Thus, there were significantly more libellulid size classes before than after fish were introduced into Pond 1 (Kolmogorov-Smirnov test, $D = 0.533$, $P < 0.001$). Size-frequency distributions of Chironomidae (Chironominae and Tanypodinae) are shown in Figure 8.2. Chironomid head width was not significantly affected by adding fish to the pond (Kolmogorov-Smirnov test, $D = 0.286$, $P = 0.343$)

Table 8.1. Macroinvertebrates (number of individuals per hand-net sweep) associated with *Vallisneria* before and after addition of fish predators in Pond 1. The percent mean effect sizes of the responses of all invertebrates and total invertebrate abundance to addition of fish are also shown. The %mean effect value of >100 depicts taxa that were absent before but present after fish were added. In brackets are the relative percent abundances. The fish were added to the pond on 16 July 2009.

Taxa	18-Jun-09	8-Jul-09	14-Jul-09	23-Jul-09	30-Jul-09	6-Aug-09	14-Aug-09	22-Aug-09	30-Aug-09	% Mean effect size
	Fishless ⟶			⟵ Fish present ⟶						
Planariidae			1.25 (4.95)	0.25 (9.09)		0.67 (6.06)	0.67 (3.64)			-36.7
Oligochaeta		0.25 (1.02)			0.50 (4.65)	0.33 (3.03)	0.33 (1.82)	0.50 (7.69)	0.50 (40.00)	333.3
Glossiphonidae				0.25 (9.09)	1.00 (9.30)			0.50 (7.69)	0.25 (20.00)	>100
Hydracarina	0.50 (0.90)		0.75 (2.97)	0.50 (18.18)		1.67 (15.15)	5.00 (27.27)			186.7
Baetidae		0.25 (1.02)								-100.0
Libellulidae	5.00 (9.01)	5.25 (21.43)	2.25 (8.91)	0.25 (9.09)	0.50 (4.65)	0.33 (3.03)				-95.7
Notonectidae	2.00 (3.60)	1.00 (4.08)	1.50 (5.94)		0.25 (2.33)					-97.2
Dytiscidae	15.00 (27.03)	2.50 (10.20)	3.50 (13.86)		1.50 (13.95)					-96.4
Chaoboridae	2.50 (4.50)				0.25 (2.33)					-95.0
Chironominae	20.00 (36.04)	13.25 (54.08)	13.75 (54.46)	1.25 (45.45)	5.75 (53.49)	6.33 (57.58)	9.00 (49.09)	4.50 (69.23)	0.50 (40.00)	-70.9
Tanypodiane	10.50 18.92	2.00 8.16	2.25 8.91	0.25 9.09	1.00 9.30	1.67 15.15	3.33 18.18	1.00 15.38		-75.4
Total number of individuals	**55.50**	**24.50**	**25.25**	**2.75**	**10.75**	**11.00**	**18.33**	**6.50**	**1.25**	**-76.0**

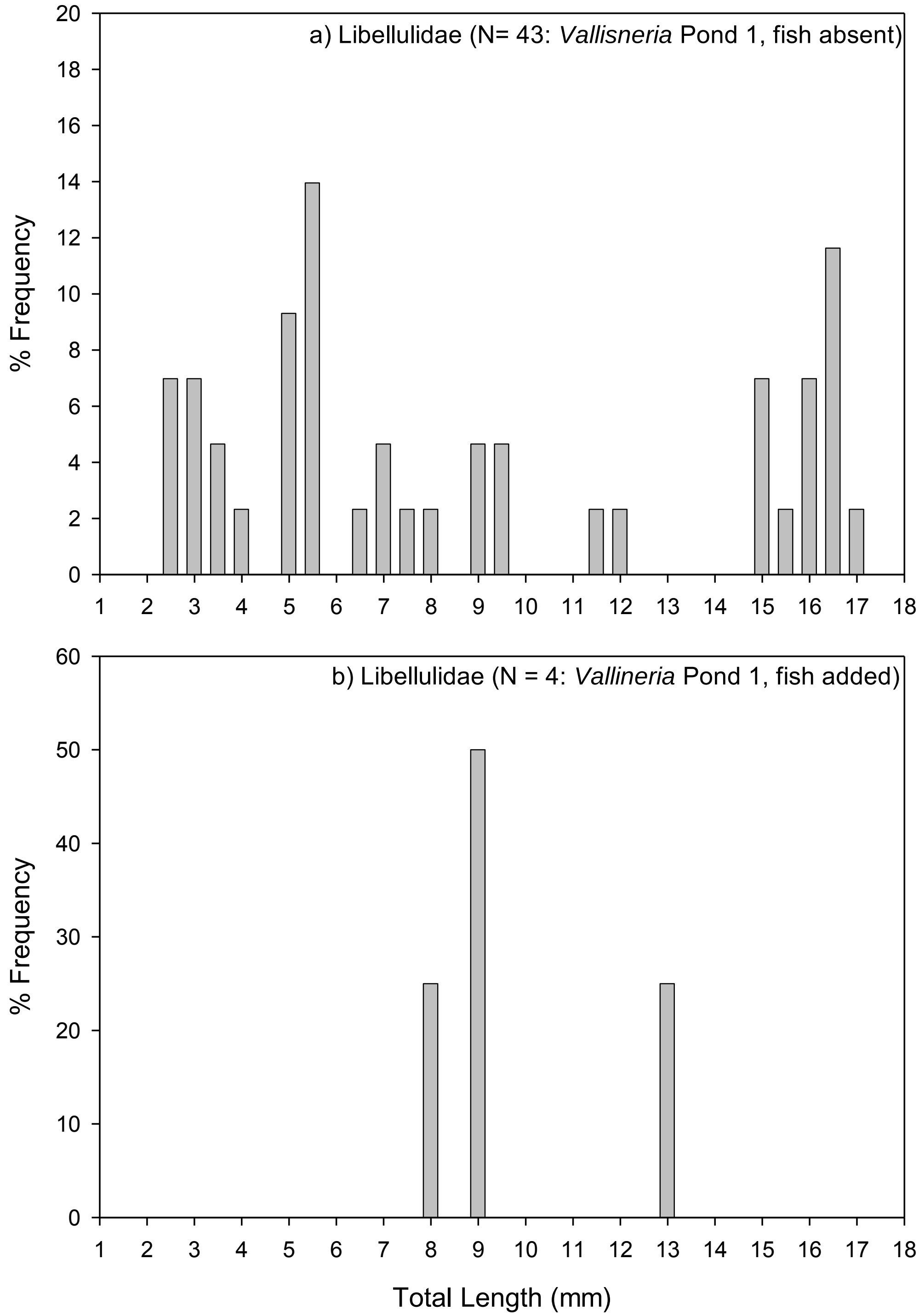

Figure 8.1. Size class frequency distribution of libellurid naiads associated with *Vallisneria*, from Pond 1, before and after adding fish.

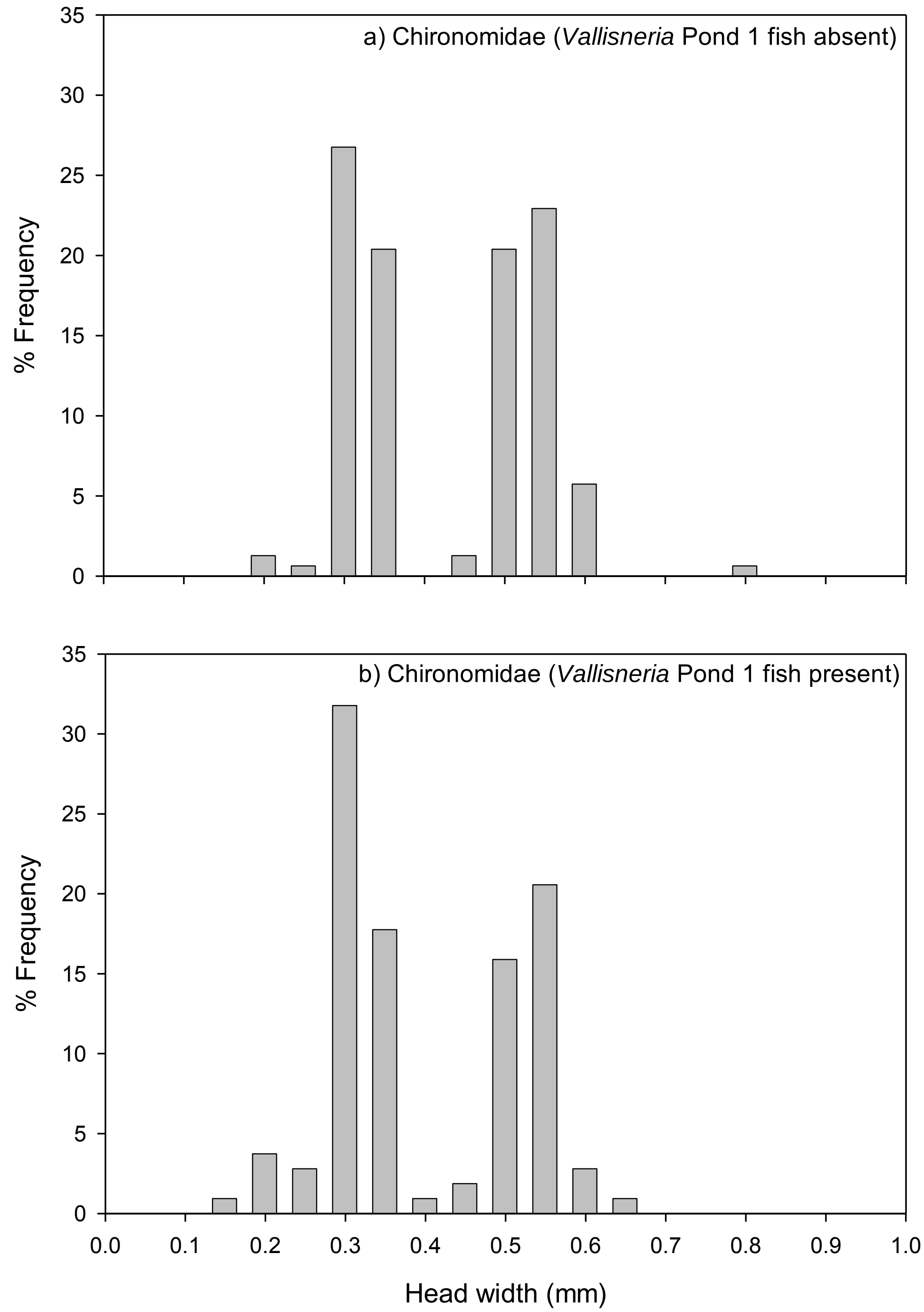

Figure 8.2: Head width size frequency distribution of Chironomidae associated with *Vallisneria*, from Pond 1, before and after adding fish.

8.3.2 **Pond 2** (*Lagarosiphon*)

Coenagrionid (28.1%) and libellulid (52.3%) naiads were the dominant taxa associated with *Lagarosiphon* before fish were introduced into Pond 2. Baetidae, Gerridae, Notonectidae and Tanypodinae were present in relatively small numbers (Table 8.2). The abundance of coenagrionid naiads decreased by 94.1%, whilst that of libellulid naiads increased by 45.4% after fish were added. Planariidae, Oligochaeta and Chironominae, which had been absent in samples collected before, were present after fish were introduced (Table 8.2). In the first week after fish were added, libellulid numbers sharply increased. Libellulid naiads (59.0%) and Chironominae larvae (21.4%) were the most abundant organisms on *Lagarosiphon* after fish added into Pond 2. An analysis of average total macroinvertebrate abundance before (56.0 $\pm$ 8.2) and after (67.3 $\pm$ 13.5) adding fish showed that addition of fish had a net positive effect (20.2%) of total invertebrate abundance (Table 8.2). Fourteen macroinvertebrate taxa were obtained after compared to ten taxa before fish were introduced into the pond. Interestingly, during the first three weeks after adding fish, the mean number of taxa was 9.7 $\pm$ 0.3, but averaged only 5.7 $\pm$ 0.7 during the last three weeks of the study period. Thus the mean number of taxa during the three weeks immediately after fish were introduced into Pond 2 was markedly greater than the three weeks before fish were introduced and the last three weeks of the study.

A broad range of coenagrionid size classes were associated with *Lagarosiphon* in Pond 2 before fish were added (Figure 8.3a). After adding fish a few small and large-bodied coenagrionid naiads were collected, but generally significantly greater numbers of moderate and large size classes were present before compared to after fish were added (Kolmogorov-Smirnov test, $P < 0.001$). Libellulid naiads during the study period were largely comprised of small size classes (Figure 8.3b) and their size class spectrum was not significantly different before and after adding fish to the pond (Kolmogorov-Smirnov test, $P > 0.05$).

8.3.3 **Pond 3** (*Vallisneria* and *Lagarosiphon*)

8.3.3.1 Invertebrates associated with *Vallisneria*

In Pond 3, which had both *Vallisneria* and *Lagarosiphon*, the macroinvertebrate community associated with *Vallisneria* before adding fish was largely comprised of Libellurid naiads (46.9%), Chironominae (13.4%) and Tanypodinae (11.5%) larvae, coenagrionid naiads (8.2%) and Hydracarina (water mites) (6.4%) (Table 8.3). After adding fish the abundances of all five taxa decreased, whilst that of planariids increased (Table 8.3). The abundances of water mites, coenagrionid naiads, and tanyponids decreased by at least 70%, whilst that of libellurid naiads and chironominae larvae decreased by 59.9% and 45.4% respectively (Table 8.3). Oligochaets, glossiphonids and baetids, which were absent in samples collected before, were obtained in small numbers in samples collected after fish were added. Coenagrionid naiads persisted for only two weeks after fish were introduced. The abundance of libellulid naiads progressively decreased but persisted up to the sixth week after fish were added. Libellurid naiads (38.7%), Chironominae larvae (30.8%) and planariids (13.7%) were the most dominant taxa when fish were present (Table 8.3).

The average total macroinvertebrate abundance after fish were introduced was markedly reduced (-62.8%) compared to before fish were added (Table 8.3). After fish were added, the number of taxa associated with *Vallisneria* gradually decreased. Average number of taxa before and after fish were added was 7.7 ± 0.9 and 5.2 ± 0.9 respectively. Total body size frequency distribution of libellulid naiads (Figure 8.4) and Chironomid head width frequency distribution (Figure 8.5) were both not significantly different before and after fish were introduced into the pond (Kolmogorov Smirnov test, $P > 0.05$).

Table 8.2. Macroinvertebrates (number of individuals per sweep) associated with *Lagarosiphon* before and after adding fish predators in Pond 2. The percent mean effect sizes of the responses of the invertebrate taxa and total invertebrate abundance to addition of fish are also shown. The %mean effect value of >100 depicts taxa that were absent before but present after fish were added. In brackets are the relative percent abundances. In brackets are the relative percent abundances. The fish were added to the pond on 16 July 2009.

Taxa	18-Jun-09	8-Jul-09	14-Jul-09	23-Jul-09	30-Jul-09	6-Aug-09	14-Aug-09	22-Aug-09	30-Aug-09	% Mean effect size
	Fishless →			← Fish present →						
Planariidae				3.0 (2.7)	1.5 2.9	1.0 (2.4)			2.0 (4.6)	>100
Oligochaeta				7.0 (6.2)	7.5 (14.3)	2.5 (6.1)				>100
Glossiphonidae					0.5 (1.0)				2.0 (4.6)	>100
Hydracarina	1.0 (2.2)					0.5 (1.2)				-75.0
Baetidae		6.0 (8.3)	5.0 (9.8)	2.0 (1.8)	0.5 (1.0)			1.0 (0.9)		-84.1
Coenagrionidae	8.0 (17.8)	17.0 (23.6)	22.0 (43.1)	5.0 (4.4)		0.5 (1.2)				-94.1
Libellulidae	29.0 (64.4)	37.0 (51.4)	21.0 (41.2)	89.0 (78.8)	34.0 (64.8)	14.5 (35.4)	26.0 (55.3)	62.5 (58.7)	27.0 (61.4)	45.4
Belostomatidae	1.0 (2.2)						1.0 (2.1)	0.5 (0.5)		-25.0
Gerridae		3.0 (4.2)	1.0 (2.0)	2.0 (1.8)	1.0 (1.9)	2.0 (4.9)				-37.5
Mesoveliade		2.0 (2.8)	1.0 (2.0)			1.50 (3.7)				-75.0
Notonectidae	1.0 (2.2)	5.0 (6.9)	1.0 (2.0)	2.0 (1.8)	2.5 (4.8)	0.5 (1.2)	1.0 (2.1)	1.0 (0.9)	1.0 (2.3)	-42.9
Chironominae				2.0 (1.8)	4.0 (7.6)	9.0 (22.0)	17.0 (36.2)	35.5 (33.3)	12.0 (27.3)	>100
Tanypodiane	2.0 (4.4)			1.0 (0.9)	0.5 (1.0)		2.0 (4.3)	4.0 (3.8)		87.5
Culicidae	1.00 (2.22)									-100.0
Total number of individuals	**43.0**	**70.0**	**51.0**	**113.0**	**52.0**	**32.0**	**47.0**	**104.5**	**44.0**	**20.2**

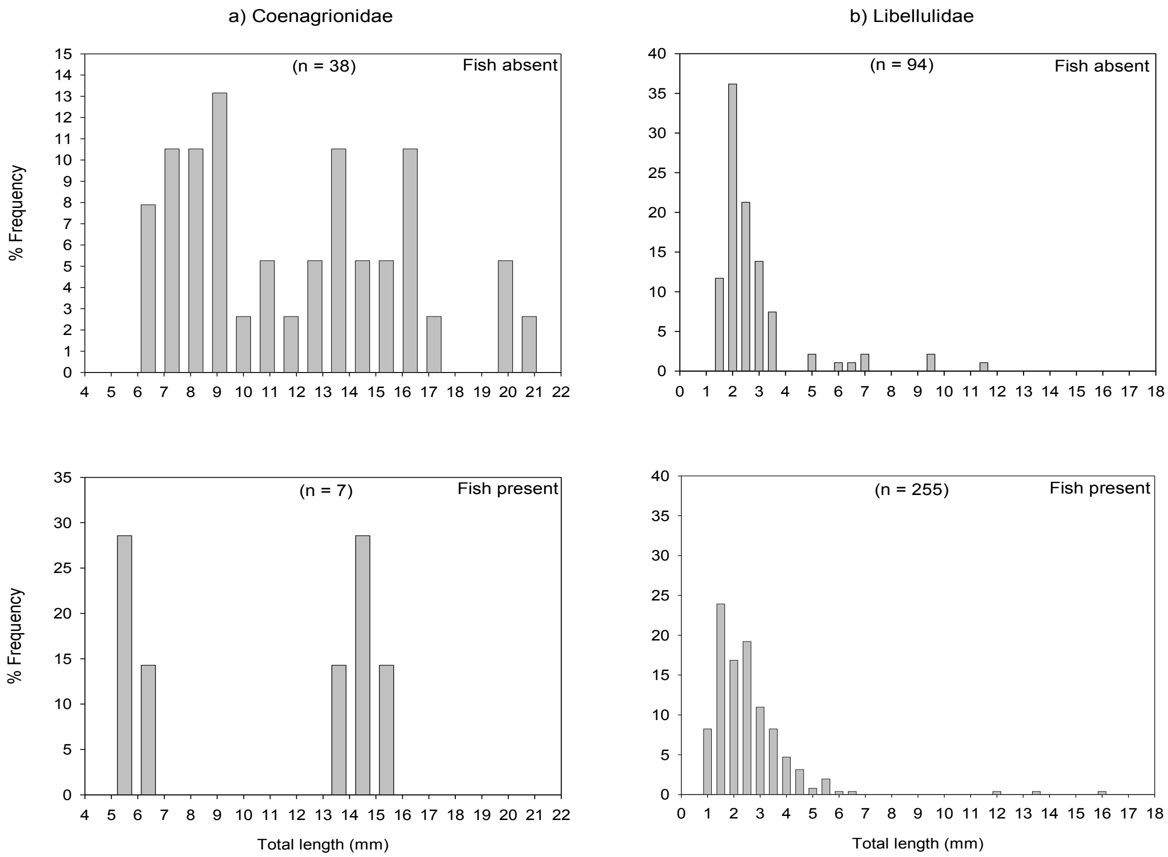

Figure 8.3. Size class frequency distribution of coenagrionid and libellurid naiads associated with *Lagarosiphon*, from Pond 2, before and after adding fish.

Table 8.3. Macroinvertebrates (number of individuals per sweep) associated with *Vallisneria* before and after addition of fish predators in Pond 3. The percent mean effect sizes of the responses of the invertebrate taxa and total invertebrate abundance to addition of fish are also shown. The %mean effect value of >100 depicts taxa that were absent before but present after fish were added. In brackets are the relative percent abundances. The fish were added to the pond on 16 July 2009.

Taxa	18-Jun-09	8-Jul-09	14-Jul-09	23-Jul-09	30-Jul-09	6-Aug-09	22-Aug-09	30-Aug-09	% Mean effect size
	Fishless →			← Fish present →					
Planariidae			1.33 (5.56)	0.50 (3.64)	2.50 (23.81)	2.00 (21.05)	1.50 (20.00)		192.5
Oligochaeta							0.50 (6.67)		>100
Glossiphonidae				0.25 (1.82)					>100
Hydracarina	2.50 (8.62)	1.00 (6.25)	1.00 (4.17)	1.25 (9.09)	1.00 (9.52)				-70.0
Baetidae					0.50 (4.76)				>100
Coenagrionidae	4.50 (15.52)	1.00 (6.25)	0.67 (2.78)	0.25 (1.82)	1.00 (9.52)				-87.8
Libellulidae	9.00 (31.03)	10.00 (62.50)	11.33 (47.22)	10.50 (76.36)	5.00 (47.62)	2.50 (26.32)	2.00 (26.67)	0.25 (16.67)	-59.9
Corixidae	1.00 (3.45)		0.67 (2.78)	0.25 (1.82)	0.50 (4.76)				-73.0
Notonectidae	1.50 (5.17)		0.67 (2.78)			0.50 (5.26)		0.25 (16.67)	-79.2
Dytiscidae			0.67 (2.78)	0.25 (1.82)					-77.5
Chaoboridae	3.50 (12.07)	1.00 (6.25)							-100.0
Chironominae	2.50 (8.62)	1.50 (9.38)	5.33 (22.22)			4.50 (47.37)	3.00 (40.00)	1.00 (66.67)	-45.4
Tanypodiane	4.50 (15.52)	1.50 (9.38)	2.33 (9.72)	0.25 (1.82)			0.50 (6.67)		-94.6
Total abundance	**29.00**	**16.00**	**24.00**	**13.75**	**10.50**	**9.50**	**7.50**	**1.50**	**-62.8**

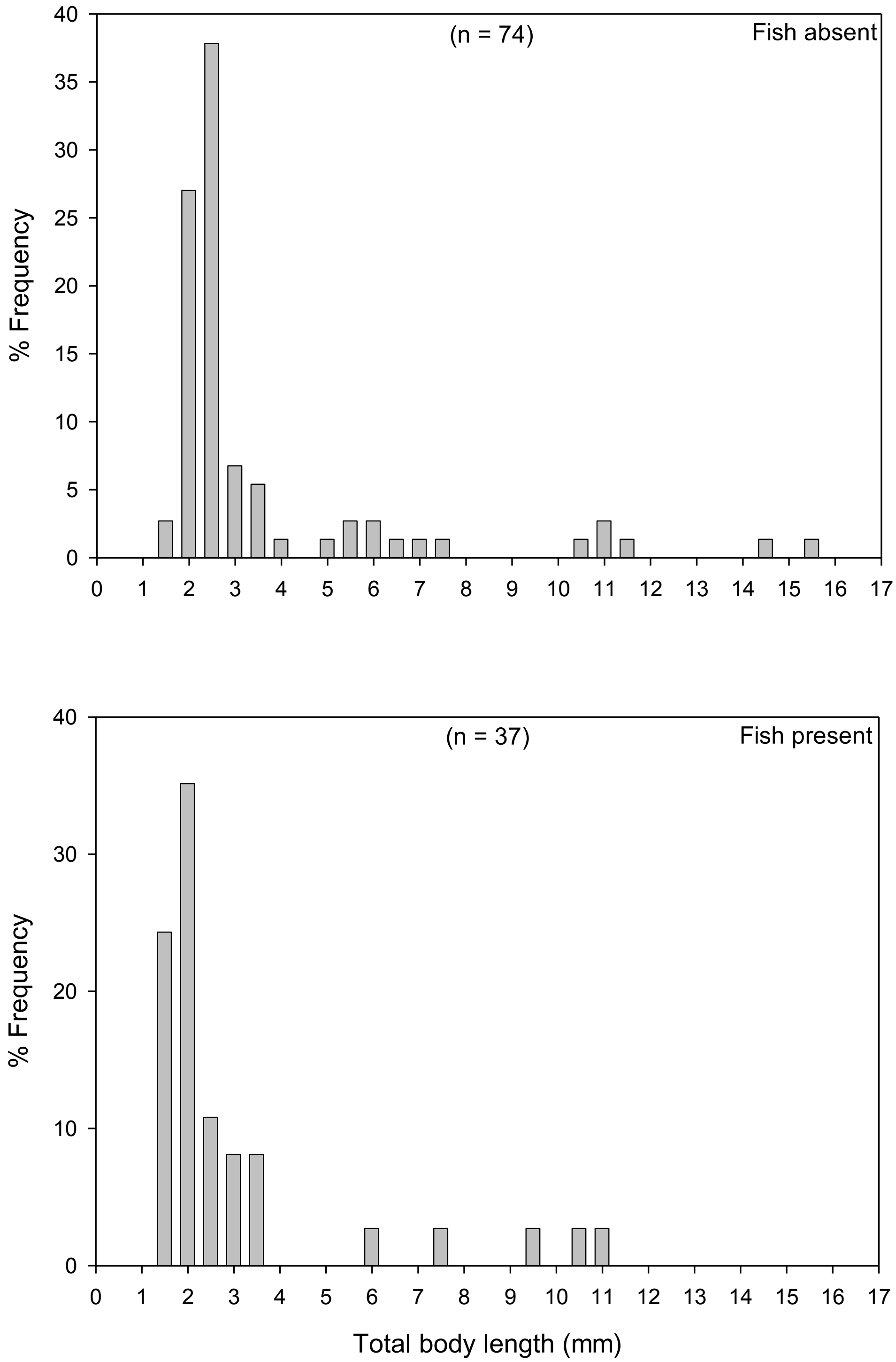

Figure 8.4. Size class frequency distributions of libellurid naiads associated with *Vallisneria* from Pond 3, before and after adding fish.

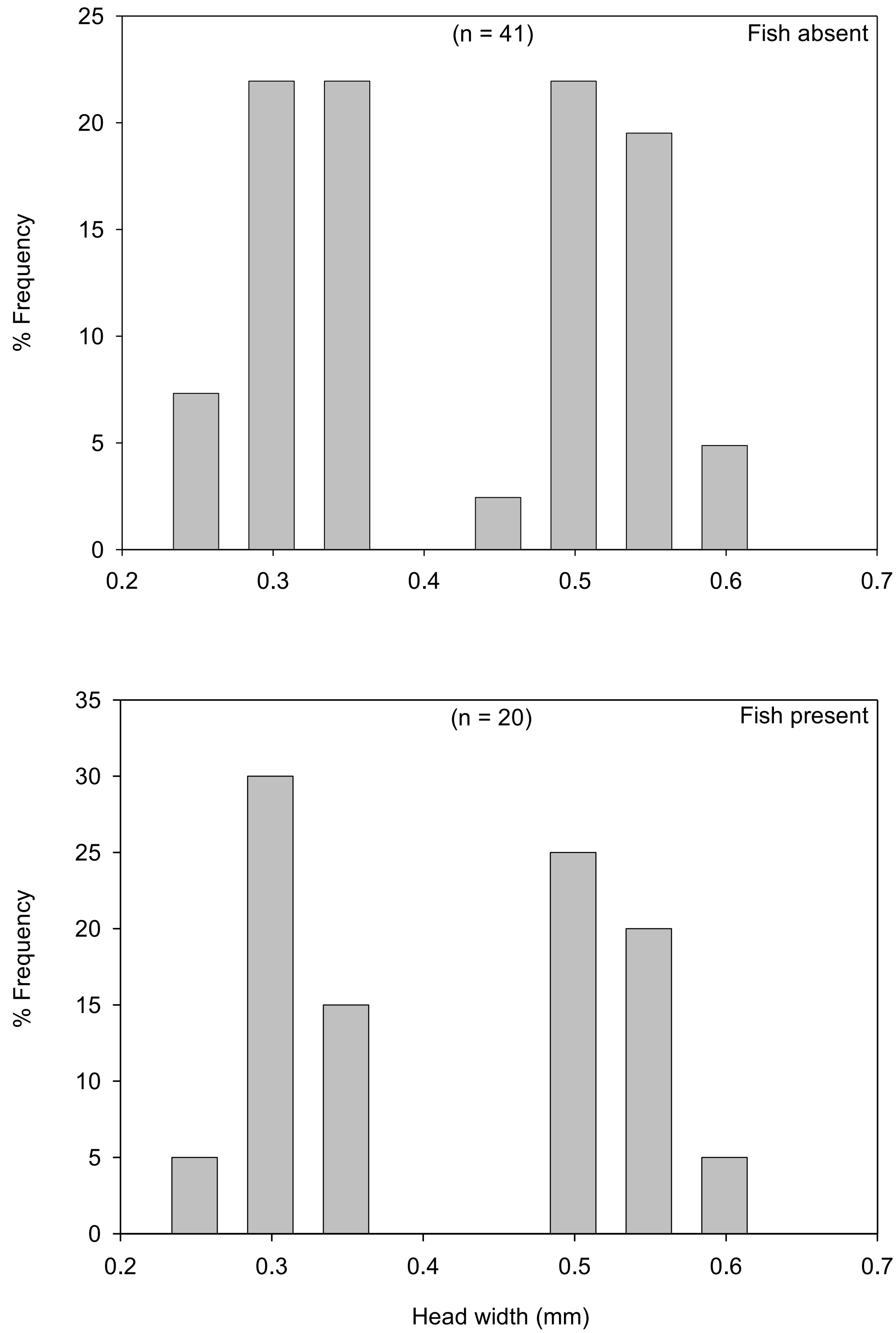

Figure 8.5. Head width size frequency distribution of Chironomid larvae associated with *Vallisneria* from Pond 3, before and after adding fish.

8.3.3.2 Invertebrates associated with *Lagarosiphon*

Libellulid (57.4%) and coenagrionid (11.9%) naiads, as well as notonectids (11.3%) were the most abundant and common taxa associated with *Lagarosiphon* in Pond 3 before fish were introduced (Table 8.4). Chironomids were rare before fish were introduced, but after introducing fish their abundance as well as that of libellulid naiads increased, while those of coenagrionid naiads, notonectids and most of the other taxa decreased (Table 8.4). The percent mean abundance of libellulid naiads increased by about 42.5% while that of Chironominae rose by 485.0% after fish were added to the pond. The macroinvertebrate assemblage associated with *Lagarosiphon* after addition of fish was largely comprised of libellulid naiads (83.3%) and Chironominae (6.9%). The overall mean macroinvertebrate abundance associated with *Lagarosiphon* decreased by about 3.6% after fish were added to the pond (Table 8.4).

The size class frequency distributions of coenagrionid and libellulid naiads that were collected from *Lagarosiphon* in Pond 3 are shown in Figure 8.6. Both coenagrionid and libellulid size class frequency distributions were not significantly different before and after introducing fish predators (Kolmogorov-Smirnov test, $P > 0.05$). Figure 8.6 also shows that libellulid naiads were generally much smaller than coenagrionid naiads during the study period.

Table 8.4. Macroinvertebrates (number of individuals per sweep) associated with *Lagarosiphon* before and after addition of fish predators in Pond 3. In brackets are the relative percent abundances. The fish were added to the pond on 16 July 2009.

Taxa	18-Jun-09	8-Jul-09	14-Jul-09	23-Jul-09	30-Jul-09	6-Aug-09	22-Aug-09	30-Aug-09	% Mean effect size
	Fishless →			← Fish present →					
Planariidae		2.0 (3.3)	3.0 (5.0)	1.0 (1.5)	1.0 (1.3)	1.0 (1.5)	2.0 (3.1)	0.5 (1.2)	-34.0
Glossiphonidae				0.5 (0.7)			1.0 (1.6)		>100
Hydracarina	3.0 (3.8)	4.0 (6.7)	1.0 (1.7)				1.0 (1.6)	0.5 (1.2)	-88.8
Baetidae					1.0 (1.3)		1.0 (1.6)		>100
Coenagrionidae	11.0 (13.9)	9.0 (15.0)	4.0 (6.7)	1.5 (2.2)	1.0 (1.3)	3.0 (4.5)			-86.3
Libellulidae	36.0 (45.6)	37.0 (61.7)	39.0 (65.0)	63.0 (92.7)	62.0 (81.6)	54.0 (80.6)	53.0 (82.8)	34.0 (79.1)	42.5
Corixidae		1.0 (1.7)		0.5 (0.7)					-70.0
Gerridae	4.0 (5.1)	1.0 (1.7)	1.0 (1.7)	0.5 (0.7)	2.0 (2.6)	2.0 (3.0)			-55.0
Mesoveliade			2.0 (3.3)	0.5 (0.7)	2.0 (2.6)	1.0 (1.5)			5.0
Notonectidae	15.0 (19.0)	6.0 (10.0)	3.0 (5.0)			3.0 (4.5)			-92.5
Pleidae	2.0 (2.5)		1.0 (1.7)						-100.0
Dytiscidae	5.0 (6.3)		3.0 (5.0)		1.0 (1.3)	1.0 (1.5)		1.0 (2.3)	-77.5
Ecnomidae			1.0 (1.7)						-100.0
Chaoboridae	1.0 (1.3)				1.0 (1.3)				-40.0
Chironominae			2.0 (3.3)	0.5 (0.7)	4.0 (5.3)	2.0 (3.0)	6.0 (9.4)	7.0 (16.3)	485.0
Tanypodiane	1.0 (1.3)								-100.0
Orthocladiinae					1.0 (1.3)				>100
Total abundance	**78.0**	**60.0**	**60.0**	**68.0**	**76.0**	**67.0**	**64.0**	**43.0**	**-3.6**

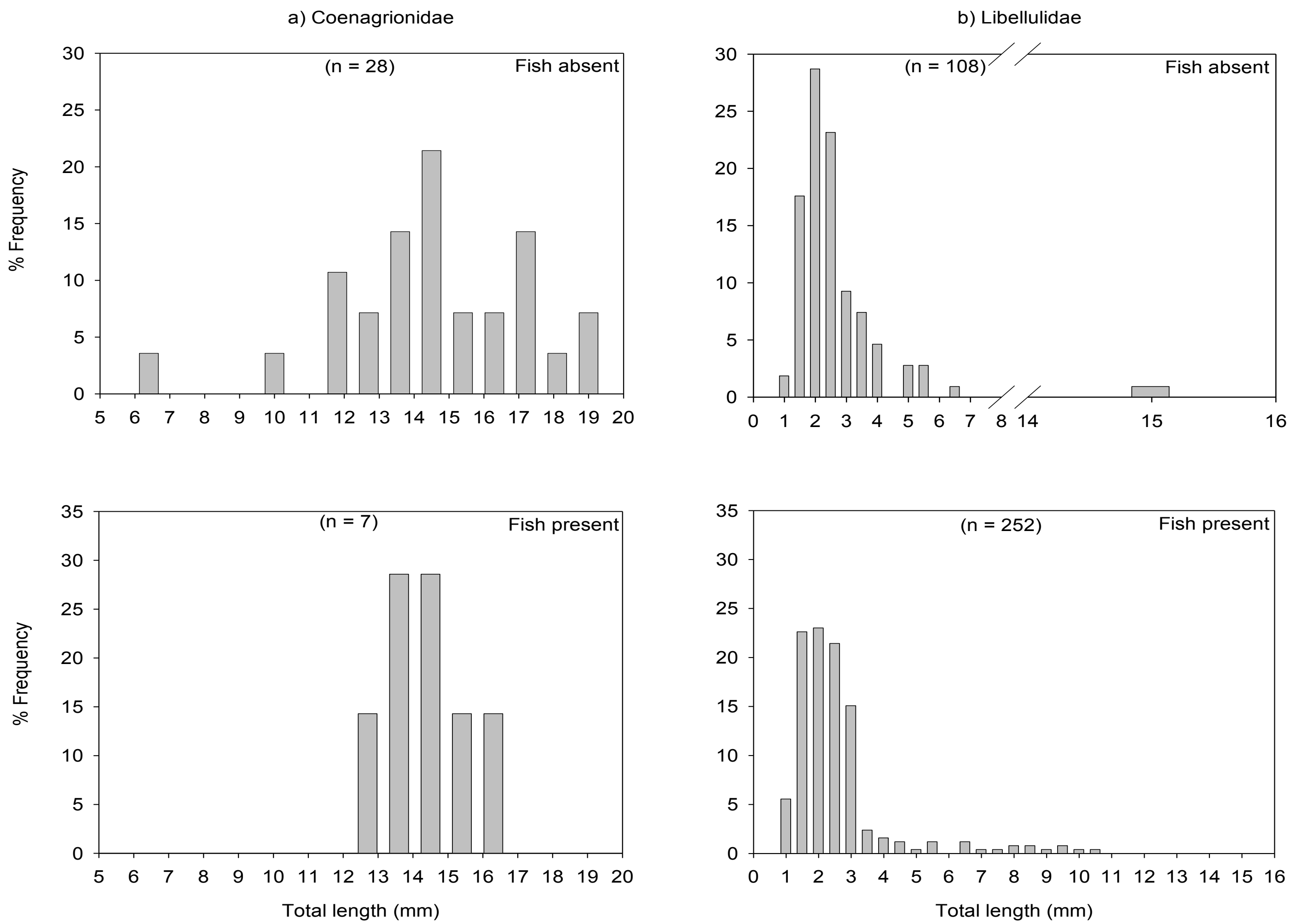

Figure 8.6. Size class frequency distributions of coenagrionid and libellurid naiads associated with ***Lagarosiphon*** **from Pond 3, before and after adding fish.**

Examination of odonate (coenagrionidae and libellulidae combined) size structure associated with *Lagarosiphon* and *Vallisneria* in Pond 3 (Figure 8.7) showed that there were significant differences in the proportion of size classes before and after fish were introduced into the pond (Kolmogorov-Smirnov test, $P < 0.01$). Large sizes were relatively more abundant on both plants before compared to after fish were added to the pond. Most of the large-bodied odonates were largely coenagrionid naiads, with libellulids generally comprised of smaller bodied early instars. After fish were added the numbers of large bodied odonates were greatly reduced on both plants. Comparing odonate size frequency distribution associated with the two plants showed that there were significant differences between the plants before as well as after fish were introduced to the pond, with larger sizes significantly more abundant on *Lagarosiphon* than on *Vallisneria* in both instances (Kolmogorov-Smirnov test, $P < 0.05$).

8.3.4 Summary of findings

The study shows that fish predation affected the macroinvertebrate community associated with both *Lagarosiphon* and *Vallisneria* in ponds. In the pond comprising only *Vallisneria* (Pond 1), large-bodied active macroinvertebrates, that is libellulid naiads, notonectids and dytiscids, virtually disappeared two to three weeks after fish were added, which resulted in the invertebrate community being dominated by small relatively inactive taxa, such as chironomids, planariids, oligochaetes. and glossiphonids. The total abundance of macroinvertebrates associated with *Vallisneria* was also greatly reduced (-76.0%) after fish were added. When *Vallisneria* was grown alongside *Lagarosiphon* (Pond 3) the macroinvertebrate community was dominated by odonates, mostly small bodied libellulid naiads and large bodied coenagrionid naiads, with relatively fewer numbers of chironomid larvae. Adding fish resulted in a sharp reduction (-62.8%) in total macroinvertebrate abundance, disappearance of coenagrionid naiads, and drastic reduction in the numbers of libellulid naiads. The invertebrate community was then largely comprised of small bodied invertebrates, mostly planariids and chironomids.

Odonate naiads were the most abundant macroinvertebrates associated with *Lagarosiphon* when it occurred as the only plant (Pond 2) or alongside *Vallisneria*

(Pond 3). In both instances appreciable numbers of large bodied coenagrionid naiads and some hemipteran taxa occurred together with greater numbers of small bodied libellulids. The numbers of small inactive taxa, planariids, glossiphonids and chironomids were generally low. After fish were added to the pond, the abundance of libellulid naiads generally increased while those of coenagrionid naiads and other active, relatively large-bodied invertebrates were greatly reduced. The abundance of small, relatively inactive taxa associated with *Lagarosiphon*, especially the chironomid subfamily Chironominae increased substantially when fish were added to Ponds 2 and 3. When *Lagarosiphon* was the only plant (Pond 2) the overall effect of adding fish on the percent mean total macroinvertebrate abundance was an increase of 20.2%. When *Lagarosiphon* was grown alongside *Vallisneria* (Pond 3), the average total macroinvertebrate abundance on *Lagarosiphon* decreased by only 3.6% after fish were added to the pond. Thus in terms of total macroinvertebrate abundances fish predation had markedly high negative impact on assemblages associated with *Vallisneria*, whilst its impact was quite minimal on assemblages associated with *Lagarosiphon*.

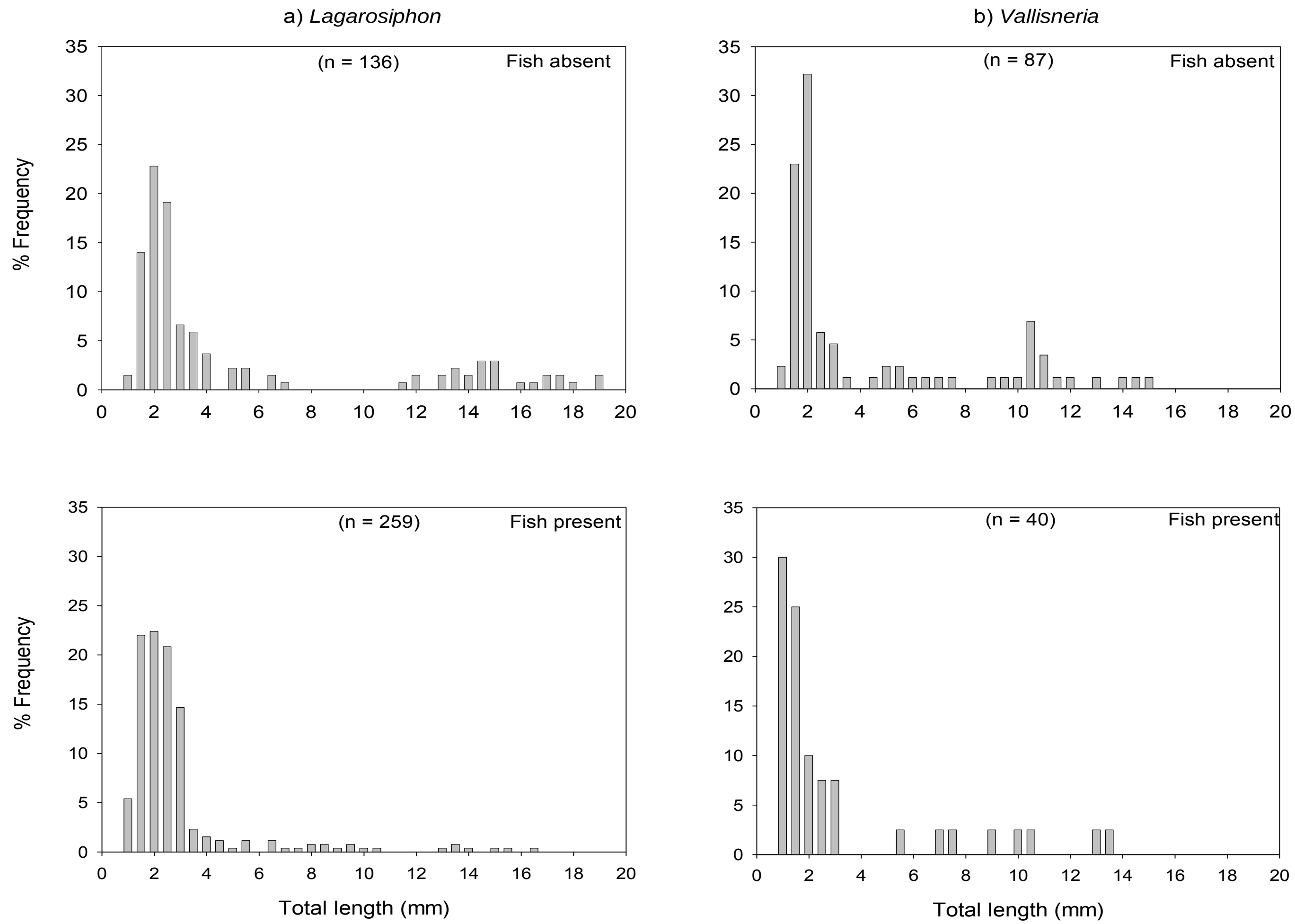

Figure 8.7. Size class frequency distribution of odonate naiads associated with *Lagarosiphon* and *Vallisneria* in Pond 3, before and after adding fish.

8.4 Discussion

Fish predation had a profound impact on epiphytic macroinvertebrates associated with both *Vallisneria* and *Lagarosiphon*, though differences in structurally complexity between the two plant species affected outcome of fish predation. There was significant reduction in total macroinvertebrate abundance as well as changes in macroinvertebrate composition on *Vallisneria*. However, adding fish predators had minimal impact on overall macroinvertebrate abundance on *Lagarosiphon*, but drastically affected macroinvertebrate community composition.

Habitat complexity is an important aspect in predator-prey interactions (Power 1992, Diehl 1992, Dahl & Greenberg 1998). Fish predation usually has greater impact in habitats with comparatively low structural complexity (Power 1990, 1992). Thus, in lakes and ponds, excluding predatory fish from the vegetated littoral zones tends to result in negligible impacts on prey abundances compared to open pelagic zones (Osenberg & Mittelbach 1996). The current study agrees to a large extent with these findings, as fish predation drastically reduced total macroinvertebrate abundance associated with the morphologically simpler *Vallisneria*, but had little impact on total abundance of invertebrates on the morphologically more complex plant, *Lagarosiphon*. Fish predation though affected macroinvertebrate community composition associated with both plants.

In the *Vallisneria* pond (Pond 1) the chironomid subfamily, Chironominae, was dominant before as well as after fish were introduced. The large predatory macroinvertebrate taxa, Libellulidae, Notonectidae and Dytiscidae were always present before, but were all removed in the presence of fish predators. Oligochaete, glossiphonids and water mites became more frequent and generally more abundant after fish were added. This suggests that the abundance of small invertebrate taxa was been suppressed through predation by larger invertebrate predators before fish were introduced. Thus fish predation had a strong negative effect on the presence of relatively large invertebrate predatory taxa in Pond 1, which indirectly enabled the establishment of greater numbers of small invertebrate taxa. Fish predation also had a strong negative effect on chironomid abundance in Pond 1, although their continued occurrence, though at relatively low abundances, suggested that there were able to coexist with the fish. According to Coffman & Ferrington (1996) chironomid may experience heavy losses through predation but generally persist because of their high reproductive capabilities.

In contrast, the insect assemblage in the *Lagarosiphon* pond (Pond 2) was characterised by the absence of Chironominae, Planariidae, Oligochaeta and Glossiphonidae, and relatively large numbers of coenagrionid and libellulid naiads when the pond was fishless. During the three weeks before fish were added there was gradual increase in the numbers of coenagrionid naiads. After fish were introduced, coenagrionid naiads were eliminated, while the abundance of the smaller-bodied libellulid naiads was not affected. Interestingly, planariids, oligochaetes, chironomines and tanypodines were common after fish were introduced. The abundance of Chironominae increased substantially after fish were introduced into the pond. Thus as in the *Vallisneria* pond (Pond 1), fish predation seemingly had an indirect positive effect on some of the small invertebrate taxa.

Batzer *et al*., (2000) found low abundances of epiphytic chironomids in marsh vegetation when predatory fish were excluded. This was attributed to increase in abundances of invertebrates such as Planorbidae and Physidae that competed for resources with chironomids, and invertebrate chironomid predators in the absence of fish predation. Although fish consumed large numbers of chironomids, their suppression of invertebrate chironomid predators and competitors had an indirect but positive impact on chironomid abundances (Batzer *et al.* 2000). The current study showed that in the absence of fish predation, Chironominae midges were absent from the *Lagarosiphon* pond (Pond 2), although Tanypodinae midges occurred in very small numbers, while in Pond 3, which had *Lagarosiphon* and *Vallisneria*, both chironomid subfamilies occurred in very small numbers on *Lagarosiphon*. The addition of fish in Ponds 2 and 3 had a negative effect on the abundance of coenagrionid naiads on *Lagarosiphon*, but was coupled with increase in chironomid abundance. In the absence of fish predation in the *Vallisneria* pond (Pond 1), Chironominae was the most abundant taxon, and Tanypodinae also occurred in relatively high numbers. In Pond 3 both midge taxa were common on *Vallisneria* before fish were added, but occurred in much reduced numbers than in Pond 1, this was especially with respect to Chironominae. Interestingly, coenagrionid naiads were completely absent from Pond 1 throughout the study period, and in Pond 3 occurred in much reduced numbers on *Vallisneria* than on *Lagarosiphon* before fish were introduced. Other predatory invertebrate taxa, e.g., libellulid naiads, notonectids and dytiscids were common before fish were added in all three ponds, as well as after fish were introduced in Ponds 2 and 3. Thus the data suggests that in the absence of fish, the main invertebrate predators of chironomids in Ponds 2 and 3 were coenagrionid naiads. Before introducing fish, the absence of coenagrionid naiads in Pond 1 enabled chironomids to flourish, and their low abundance on *Vallisneria* in Pond 3, allowed considerable chironomid numbers to occur. Introducing fish resulted in reduction and eventual removal of coenagrionid naiads from Ponds 2 and 3, which had an indirect positive effect on the abundance of chironomids and other small taxa.

In all three ponds relatively large odonate naiads were the dominant invertebrate predators before fish were introduced. Odonates are normally the most dominant invertebrate predators in fishless freshwater environments (Morin 1984a, b) and intraguild predation is common (Morin 1984b, Robinson & Wellborn 1987). The study illustrates the possible effect of intraguild predation on macroinvertebrate community structure and body size distribution in fishless aquatic environments. The body length of most of libellulid naiads (>80%) associated with *Lagarosiphon* in Ponds 2 and 3 was less than 4mm. In contrast the size-class range of coenagrionid naiads was broader and much more evenly distributed, with 42.1%, 31.6% and 26.3% of individuals less than 10 mm, greater than 10 mm but less than 15mm, and greater than 15 mm respectively. Coenagrionid naiads did not occur on *Vallisneria* in Pond 1, and 23.3% of libellulid naiads had total body length of greater than 15mm. Thus, where coenagrionids were absent, a relatively greater number of libellulid naiads were able to grow to large sizes. The results suggests that although libellulids had colonised and established themselves in Ponds 2 and 3 before fish were added, predation by coenagrionid naiads suppressed their development such that only a few could grow to large sizes. Thus, intraguild predation among odanates was an important factor in structuring macroinvertebrate in the absence fish predators.

The study also shows an aspect of the effect of size-selective predation by fish on macroinvertebrate community structure. The primary mode of prey detection by many littoral fish is visual (Croy & Hughes 1991), with greater preference for large prey (Wellborn *et al.* 1996). Before fish were added, the numbers of non-predatory macroinvertebrates were very low in Ponds 2 and 3, which was due to the impacts of large predatory invertebrates. Prejs *et al.* (1997) also found very high numbers of predatory invertebrates and drastically reduced numbers of non-predatory epiphytic invertebrates when they removed fish from a small lake. In this study adding fish predators to the ponds initially resulted in a reduction in the numbers of the largest invertebrate predators in all ponds. In Pond 1, libellulid naiads, notonectids and dytiscids were removed. On *Lagarosiphon*, in both Ponds 2 and 3, Coenagrionidae was the taxon most severely impacted by fish predation. A week after adding fish to Ponds 2 and 3, there was a sharp increase in the abundance of small libellulid naiads on *Lagarosiphon*. The increase in libellulid abundance was not observed on *Vallisneria* in Ponds 1 or 3, thus also supporting the earlier assertion that intraguild predation by the larger coenagrionid naiads was suppressing development libellulids. Although libellulid abundance fluctuated, fish predation did not seem to have a significant impact on their numbers on *Lagarosiphon*. When odonates from Pond 3 where pooled and considered together (Figure 8.7) the effect of fish predation was most severe on large bodied classes on both plants.

This study illustrates that differences in structural complexity between *Vallisneria* and *Lagarosiphon* has a bearing on the effects of predatory macroinvertebrates and fish on non-predatory epiphytic macroinvertebrates. It shows and agrees with the findings of Chapter 7 that in fishless waters, odonates are generally the top predators associated with both plants, but also that invertebrate predation may significantly affect the invertebrate assemblage structure. Structural simplicity of *Vallisneria* results in the establishment macroinvertebrate assemblage characterised by relatively low total abundance, few predatory macroinvertebrate taxa and dominance by small taxa such as chironomids. The study suggests that fish predation tends to decimate macroinvertebrate communities on *Vallisneria*. In contrast, the structural complexity of *Lagarosiphon* results in comparatively much greater total macroinvertebrate abundance and enables the coexistence of a greater number of predatory macroinvertebrate taxa, dominated by odonates when fish are absent. The study also shows that fish predation may have minimal impact on total macroinvertebrate abundance associated with *Lagarosiphon*, but may affect invertebrate assemblage composition through size-selective predation. Also notable is that suppression of large predatory invertebrate has positive effects on epiphytic chironomid abundance.

8.4.1 Conclusions

Although the results obtained in this study may not be entirely applicable to the large and more open environment of the shallow marginal zones of Lake Kariba, they do raise some interesting questions as well as give probable explanations for others. The current chapter and Chapter 7 both support the view that differences in epiphytic macroinvertebrate community composition of *Vallisneria* and *Lagarosiphon* observed in Lake Kariba (Chapter 3) are largely due to differences in structurally complexity between the plants. It is shown here that fish predation affects epiphytic macroinvertebrates on both plants. The impact of fish predation results in very low abundances of large bodied and generally low overall abundance of macroinvertebrates associated with *Vallisneria*. Thus the comparative low macroinvertebrate abundance noted on *Vallisneria* in Lake Kariba (Chapter 3) was probably due to its low structural complexity, which enables fish predators easier access to epiphytic invertebrates. This study suggests that fish predation has negligible effect on total macroinvertebrate abundance associated with *Lagarosiphon* in Lake Kariba, but affects the macroinvertebrate community through size-selective predation on large mobile predatory macroinvertebrates. Coenagrionid naiads are shown to be a major predator especially of epiphytic chironomids on *Lagarosiphon*, and that when fish are absent they are capable of drastically reducing chironomid numbers. The study suggests that there is close interaction between fish predation, coenagrionid naiad presence and establishment of chironomids on *Lagarosiphon*, with the negative effects of fish predation on coenagrionids indirectly benefiting chironomids. The study also gives a possible explanation for the low numbers and occurrence of libellulid naiads that were associated with *Vallisneria* and *Lagarosiphon* in Lake Kariba. It is shown that coenagrionid naiads do prey on other odonates and can suppress their numbers on both plants.

Thus epiphytic macroinvertebrates in Lake Kariba are involved in complex and dynamic interactions with their habitats, each other as well as other biotic components such as fish. Further studies including fish exclusion experiments in the lake are necessary to advance our understanding of these interactions. In Chapter 9 I assess the aspect of the effect of variation in fish density on invertebrates associated with *Lagarosiphon*.

CHAPTER 9

AN ASSESSMENT OF SHORT-TERM SURVIVORSHIP OF *Ischnura* (ODONATA: COENAGRIONIDAE) NAIADS AT DIFFERENT DENSITIES OF JUVENILE FISH (*Oreochromis niloticus*)

9.1 Introduction

Coenagrionids are the most common and abundant odonates associated with *Lagarosiphon* in Lake Kariba and three genera, *Pseudagrion* sp., *Enallagma* sp. and *Ischnura* sp., tend to occur in approximately equal numbers (Chapter 4 of this thesis). They are the dominant large invertebrate predators associated with *Lagarosiphon*. In Chapter 5 of the current thesis it was shown that damselfly naiads are present throughout the year and together with chironomid larvae dominate total insect biomass on *Lagarosiphon*. Several studies in freshwater systems (e.g., Nyström & Åbjörnsson 2000, Chapters 7 and 8 of this thesis) have shown that large predatory invertebrates have strong negative effects on prey species abundances. Odonate naiads can have a marked effect on other freshwater organisms as they are able to attack and consume a wide range of invertebrate prey, and larger-bodied species can also prey on smaller vertebrates (Rowe 2006). Since invertebrates make up an important food source for a number of freshwater fish species and odonate naiads are important prey for fish (Rask 1986), it is likely that coenagrionid naiads play an important role in food-web dynamics of the littoral zone of Lake Kariba.

Fish predation can have strong negative effects on invertebrate abundances in freshwater systems (e.g., Diehl 1992, Nyström *et al.* 2001, Åbjörnsson *et al.* 2002, Chapter 8 of this thesis). Because fish predators generally tend to be size selective (Wellborn *et al*. 1996) the abundances of large-sized invertebrates, especially large predatory taxa tend to be reduced when fish predators are present (Diehl 1992, Batzer *et al.* 2000, Chapter 8 of this thesis). In the tropics and subtropics large numbers of juvenile fish and small-bodied fishes tend to occur all year round in the littoral zone of freshwater bodies and apply strong predation pressure on invertebrates (Iglesias *et al.* 2007, Van Leeuwen *et al.* 2007, Teixeira-De Mello *et al.* 2009).

Oreochromis niloticus Linnaeus, the Nile tilapia, is an omnivorous African fish. It is an important aquaculture fish and has been successfully introduced into many tropical and subtropical lakes and reservoirs in many parts of the world. It was introduced in Lake Kariba in the 1990s when it escaped from aquaculture cages and is now one of the most dominant fish species in inshore waters of the Sanyati Basin. Large numbers of juvenile *O. niloticus* normally occur in the vegetated regions of shallow inshore waters (pers. obs.) Although originally described as being primarily herbivorous (Moriarty & Moriarty 1973, Getabu 1994), recent studies done in Lake Victoria have shown *O. niloticus* to be omnivorous, as it feeds on a broad range of food items, including a high proportion of macroinvertebrates (Gophen *et al.* 1993, Balirwa 1998, Bwanika *et al.* 2006, Njiru *et al.* 2004). Its successful colonization of many freshwater systems around the globe has largely been attributed to its broad diet, such that food is rarely a limiting factor, and its flexibility in growth rate and maturation size, which vary according to prevailing environmental conditions (Balirwa 1998, Lévêque 2002, Bwanika *et al*. 2006).

This study was initiated to assess the effect of *O. niloticus* juveniles on *Ischnura*, one of the three common and abundant damselfly taxa associated with submerged macrophytes in Lake Kariba. The purpose of study was to determine the effect of varying densities of *O. niloticus* juveniles (< 5 cm) on survivorship over short periods of different size classes of *Ischnura* naiads in moderately dense *Lagarosiphon* beds. I hypothesised that small-sized *Ischnura* naiads would be more susceptible to predation and their percent survival much reduced compared to moderate- and large-sized naiads. This was based on the assumption that the small mouth gapes of the juvenile fish would largely limit them to preying on small-bodied naiads. I also hypothesised that percent survivorship of all naiad size classes would decrease as fish density was increased.

9.2 Materials and Methods

The experiment was done over a period of six days in small glass aquaria, eight of which had a bottom surface area of 0.0625 m^2 and three had an area of 0.2 m^2 (section 2.3.7). *Oreochromis niloticus* juveniles (total length range 2.8 – 4.6 cm) were collected using seine netting from Lake Kariba. The fish were kept in an aerated storage aquarium and fed on live invertebrates collected from *Lagarosiphon* on days 2 and 3 after been netted. On the fourth day the fish were not fed. Segments of *Lagarosiphon* that had been thoroughly washed using tap water and each attached to a lead weight were randomly arranged in each aquarium so that a number of lengths of 10-cm-long fronds of the plant stood in the filtered pond water in each tank. The density of plants was 575 - 576 fronds per m^2 in all the aquaria. Details are provided in table 10.1. On the fifth day of the experiment small (< 5 mm), moderate (5-10 mm) and large-sized (length > 10 mm) *Ischnura* naiads were added to the aquaria. In each of the 8 small aquaria 20 small-, 20 moderate- and 10 large-sized naiads were added. In all the three larger aquaria 64 small-, 64 moderate- and 20 large-sized naiads were stocked. Two hours after stocking the naiads, fish were added at densities of 0, 32, 64 and 255 per m^2. Two tanks were kept as controls, with no fish added, while the other fish density treatments had three replicates. The highest fish density treatment was replicated in the three larger aquaria. The numbers and sizes of naiads surviving in each aquarium 24-hours after fish were added were counted and recorded. Details of the materials and methods are given in section 2.3.7.

9.3 Results

9.3.1 *Lagarosiphon* leaf density

The mean leaf density per stem ranged from 16.7 to 20.8 per cm of *Lagarosiphon* (Table 10.1) and there were no significant differences in leaf density among the eleven ponds (ANOVA [log x transformed] ($F_{10, 139} = 1.602$, $p = 0.113$).

Table 10.1: Description of the arrangement of *Lagarosiphon* in the eleven aquaria. [1] n = 10 unless otherwise stated

Aquarium	Area of bottom surface (m^2)	# of stems	Stem density ($\#/m^2$)	Mean leaf density (#/cm of stem)[1]
1	0.0625	36	576	18.8 ± 0.5
2	0.2	115	575	17.6 ± 0.7 (n = 20)
3	0.0625	36	576	17.6 ± 0.7
4	0.0625	36	576	18.1 ± 0.8
5	0.0625	36	576	18.5 ± 1.3
6	0.2	115	575	16.7 ± 0.6 (n = 20)
7	0.0625	36	576	17.7 ± 0.5
8	0.0625	36	576	18.2 ± 0.8
9	0.2	115	575	16.9 ± 0.5 (n = 20)
10	0.0625	36	576	17.0 ± 0.8
11	0.0625	36	576	20.8 ± 1.5

9.3.2 Survivorship of naiads at different fish densities

The number of each size class in the eleven aquaria before and 24 hours after fish were added as well as the percent survival of the naiads in each aquaria are shown in Table 10.2. Figure 10.1 shows the variation in mean percentage survivorship of the three size classes of naiads at the different densities of juvenile *O. niloticus*. All three naiad size classes had the lowest mean percent survivorship at high fish densities (i.e. 255 fish per m^2).

9.3.2.1 Small-sized naiads

Percent survivorship of small-sized naiads was lowest at high fish densities (Figure 10.1) and there were significant differences in survivorship of naiads among the different fish densities (ANOVA $F_{3, 11} = 36.79$, $p < 0.01$). Percent survivorship was significantly less at the highest fish density (255 fish per m^2) compared to all the other three fish densities (Tukey Q-test, $p < 0.01$). Survivorship of naiads did not differ significantly in aquaria with fish density of 32 fish per m^2 compared to aquaria in which fish were not added (Tukey Q-test, $p > 0.05$). At the density of 64 fish per m^2, survivorship was significantly less compared to when fish were absent (Tukey Q-test,

$p < 0.01$), while there were no significant differences in survivorship at densities of 32 and 64 fish per m^2 (Tukey Q-test, $p > 0.05$).

9.3.2.2 Moderate-sized naiads

Fish density had a significant effect on percent survivorship of moderate-sized naiads (ANOVA $F_{3, 11} = 45.50$, $p < 0.01$). At fish densities of 0, 32 and 64 per m^2 there were no significant differences in percent survivorship of naiads (Tukey Q-test, $p > 0.05$). The survivorship of moderate-sized naiads at fish density of 255 per m^2 was significantly less compared to the other fish densities (Tukey Q-test, $p < 0.01$).

9.3.2.3 Large-sized naiads

The short-term mean percent survivorship of large-sized naiads was significantly greater in aquaria without fish compared to those with fish densities of 32, 64 and 255 per m^2 (ANOVA, $F_{3, 11} = 63.69$, $p < 0.001$; Tukey Q-test, $p < 0.001$). Survivorship at 32, 64 and 255 fish per m^2 was generally low and there were no significant differences among the three fish densities (Tukey Q-test, $p > 0.05$).

Table 10.2. The densities of juvenile *O. niloticus* and numbers of the three naiad size classes before and 24-hours after fish were added to aquaria. Percent survivals of naiads in the aquaria are also shown.

Fish density (no./m^2)	**Number and size of naiads in aquaria**						**% Survival of naiad size classes**		
	Before adding fish			**24-hours after adding fish**					
	Small	Moderate	Large	Small	Moderate	Large	Small	Moderate	Large
0	20	20	10	16	19	10	80	95.0	100
0	20	20	10	15	17	10	75	85.0	100
32	20	20	10	10	20	3	50.0	100.0	30
32	20	20	10	15	16	0	75.0	80.0	0
32	20	20	10	11	17	0	55.0	85.0	0
64	20	20	10	8	18	1	40.0	90.0	10
64	20	20	10	9	15	0	45.0	75.0	0
64	20	20	10	9	18	2	45.0	90.0	20
255	64	64	20	8	19	1	12.5	29.7	5
255	64	64	20	8	12	0	12.5	18.8	0
255	64	64	20	14	18	0	21.9	28.1	0

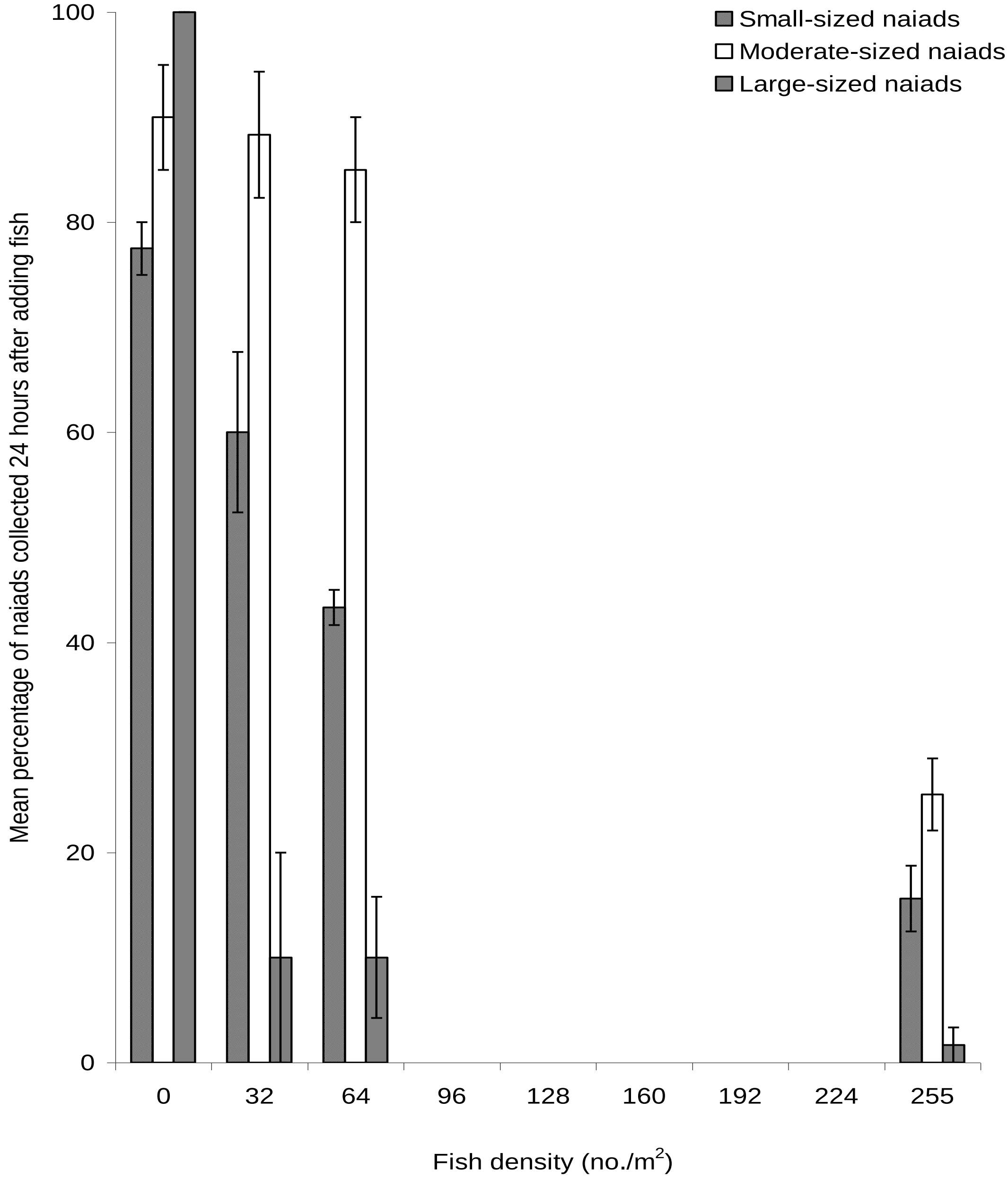

Figure 9.1. Mean percent survival (± standard error) of the three *Ischnura* naiad size classes over a 24-hour exposure period to different densities of *O. niloticus* juveniles.

9.3.3 Comparison of survivorship of different naiad size classes

9.3.3.1 "No fish" treatment

The survivorship of naiads in aquaria that had no fish added during the experimental period differed significantly among the three size classes (ANOVA, $F_{2, 8} = 29.40$, $p < 0.01$). The mean percent survivorship of large-size naiads was significantly greater compared to small and moderate sizes (Tukey Q-test, $p < 0.05$), while percent survivorship of moderate-sized naiads was significantly greater than small sizes (Tukey Q test, $p < 0.05$).

9.3.3.2 Fish density (32 per m^2 treatment)

At the fish density of 32 per m^2 mean percent survivorship differed significantly among the three size classes (ANOVA, $F_{2, 8} = 24.27$, $p < 0.01$). The survivorship of small- and moderate-sized naiads was not significantly different (Tukey Q-test, $p > 0.05$) but both were significantly greater than large-sized naiads (Tukey Q-test, $p < 0.05$).

9.3.3.3 Fish density (64 per m^2 treatment)

The mean percent survivorship differed significantly among the three naiad size classes at density of 64 fish per m^2 (ANOVA, $F_{2, 8} = 69.32$, $p < 0.01$). Moderate-sized naiads had significantly greater mean percent survivorship than small- and large sized naiads, while the survivorship of small-sized individuals was significantly greater than that for large-sized naiads (Tukey Q-test, $p < 0.01$).

9.3.3.4 Fish density (255 per m^2 treatment)

Survivorship of the three naiad size classes was also significantly different at the highest fish density used during the study period (ANOVA, $F_{2, 8} = 17.80$, $p < 0.01$). The mean percent survivorship of small- and moderate-sized naiads were not significantly different (Tukey Q-test, $p > 0.05$), but both had significantly greater mean percent survivorship than large-sized naiads (Tukey Q-test, $p < 0.05$).

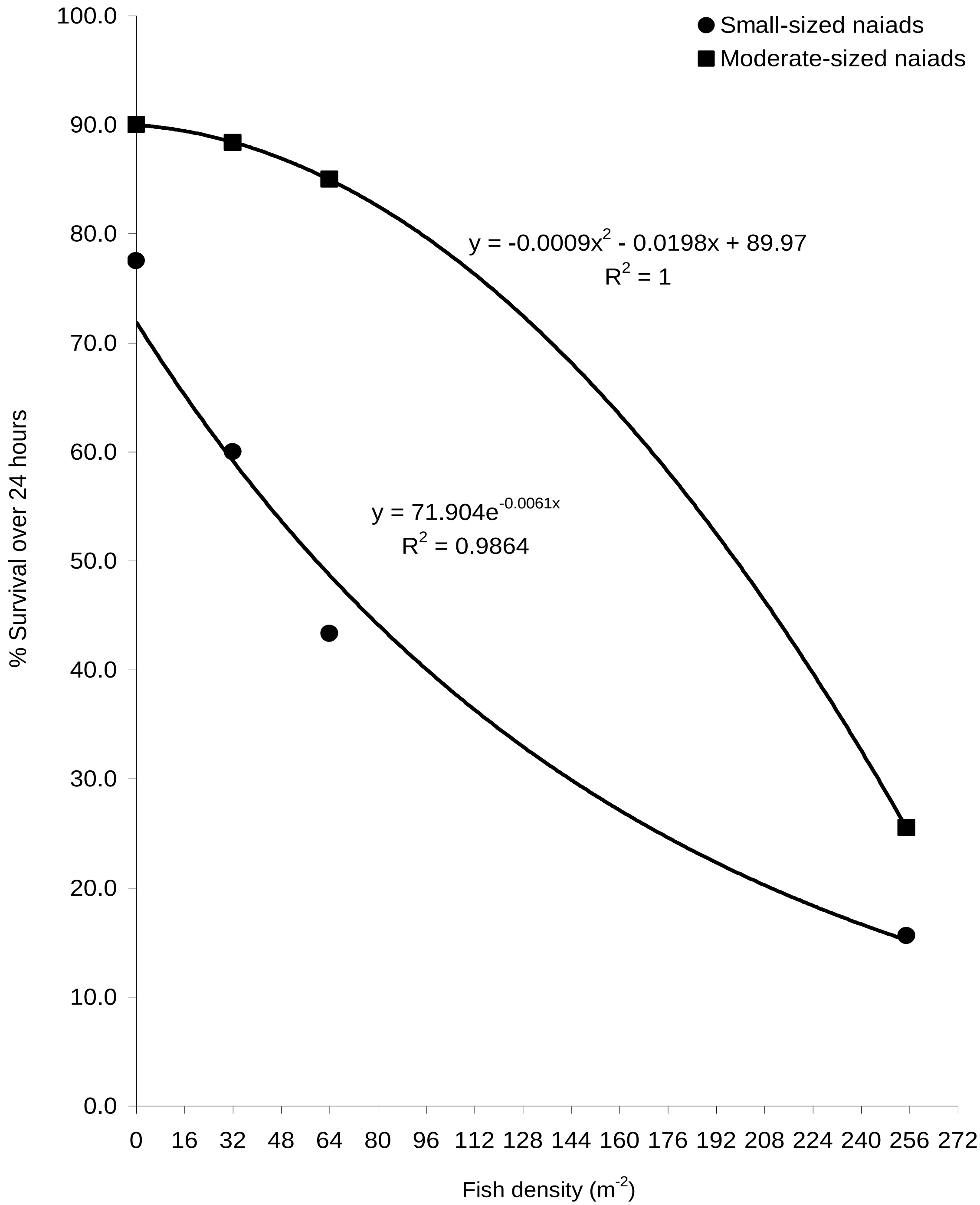

Figure 9.2: Trend lines and the formulas relating percent survival of small- and moderate-sized *Ischnura* **naiads at different densities of juvenile** *O. niloticus*.

9.3.4 Estimated fish densities at which 50% of naiad survived

Figure 9.2 shows the trends in mean percent survival of small and moderate-sized with increase in the density of *O. niloticus* juveniles. The calculated fish densities at which the short-term survival of small and moderate-sized individuals was 50% were about 60 m^{-2} and 200 m^{-2} respectively. For large-bodied naiads short-term survival was less than 50% even at the lowest fish density (32 m^{-2}) that was used in the study.

9.4 Discussion

9.4.1 Effect of *O.niloticus* juveniles on short-term survival of *Ischnura* naiads associated with *Lagarosiphon*

In a study done on Lake Victoria (East Africa) Njiru *et al.* (2004) suggested that small sizes (< 5cm) of *O. niloticus* did not feed on insects because of their small mouth gape. In the current study I had therefore originally anticipated that small-sized *Ischnura* naiads (< 5mm) would be more vulnerable to predation by juveniles of *O. niloticus* than moderate and large-sized naiads. The study showed that juveniles of *O. niloticus* that are less than 5 cm do indeed feed on insects. Fish predators tend to be size selective and largely consume the largest individuals across the range of prey sizes that they are physically able to ingest (Dixon & Baker 1988, Wellborn 1994, Wellborn *et al.* 1996). Thus, the greatest impact of fish predation generally tends to be on large-bodied prey (Wellborn *et al*. 1996). The current study showed that short-term survival of large-bodied naiads was 100% in the absence of fish but in the presence of fish was equally low throughout the density spectrum suggesting extremely high vulnerability of large-bodied naiads. Thus in the absence of other food items, size-selective predation by *O. niloticus* juveniles, results in a disproportionately greater negative effect on large-bodied *Ischnura* naiads compared to small and moderate-bodied naiads.

Interestingly the study also showed that fish predation had a significant negative impact on moderate-sized naiads at very high densities (255 m^{-2}) and a negligible effect at lower densities (i.e. 32 and 64 m^{-2}). The calculated fish density that would have resulted in 50% survival of moderate-sized naiads was about 200 m^{-2}. Comparatively, the short-term survival of small-sized naiads was significantly impacted at very high fish density (i.e., 255 m^{-2}) as well as at 64 m^{-2} and a fish density of about 60 m^{-2} would have resulted in 50% survival. Thus the results suggest that at low to moderate fish densities small-sized *Ischnura* naiads are more vulnerable to predation by juvenile *O. niloticus* compared to moderate-sized naiads.

According to Wellborn *et al*. (1996) size-selective predation is a behavioural adaptation to maximise foraging gain. Thus since juvenile *O. niloticus* preferred bigger naiads over the moderate and small-bodied ones it is logical to assume that once the numbers of large-bodied naiads had drastically reduced, moderate-sizes should have been preferred and thus more susceptible to predation than small-sizes. Prey behaviour, including level of activity (Convey 1988, Johnson 1991, Welborn *et al*. 1996) and intra- and inter-specific interactions of prey animals (Lima & Dill 1990, Swisher *et al.* 1998, Elkin & Baker 2000) within the refuge tend to affect the level of mortality due to predation. Fish predators are generally more likely to attack active than inactive prey (Baker & Smith 1997, Wellborn *et al.* 1996). The current study showed that in the absence of fish predation, the mean percent short-term survival of large-bodied naiads (100%) was significantly greater than that for small- and moderate-sizes. The average percent survival of moderate-sizes was also significantly greater than that of small-sizes in aquaria without fish. These results suggest that larger naiads preyed on smaller ones. Baker *et al*. (1999) showed that interactions between naiads of *Ischnura verticalis* increased the swimming activities, which according to Elkin & Baker (2000) increases their susceptibility to fish predation. The results of the current study suggest that small-bodied naiads were probably more active in the presence of bigger naiads, which in turn made them more vulnerable to fish predation than the moderate-sized naiads were.

In this study I assessed the short-term survival at different densities of juvenile *O. niloticus* of small-, moderate- and large-bodied naiads of *Ischnura* from Lake Kariba in aquaria with similar densities of *Lagarosiphon*. The study demonstrated that juvenile *O. niloticus* (< 5 cm) can prey on large individuals of *Ischnura*. It showed that in moderately dense beds of *Lagarosiphon*, large-bodied naiads are more susceptible to predation by *O. niloticus* and their percent survival is generally much lower than small and moderate sizes even at low fish densities. Thus juvenile *O. niloticus* maximised foraging by selecting for large and probably more visible naiads. The negative effect of fish predation on small- and moderate-sized naiads generally increased as fish density was increased. The study demonstrated that as fish density increases small individuals may generally be more vulnerable than moderate-sized ones because of intraspecific interactions such as cannibalism, which make small-sizes more active and so prone to fish attack than moderate-sized naiads.

The main limitation of this study was that only one type of prey was presented to *O. niloticus*, though different sizes of prey were available. In Lake Kariba, chironomid larvae are the most abundant insects associated with *Lagarosiphon* in shallow inshore waters (Chapter 4 of this thesis). According to Vázquez & Aizen (2003) predators generally tend to prefer most abundant prey species. In studies done in East Africa on Lake George (Moriarty & Moriarty 1973) and Lake Victoria (Getabu 1994, Njiru *et al.* 2004), the contribution of insects to the diet of small *O. niloticus* (< 5cm) was negligible and zooplankton was the dominant food item. In another study on Lake Nabugabo, a satellite of Lake Victoria, Bwanika *et al.* (2006) showed that the diet of juvenile *O. niloticus* (< 10cm) was largely dominated by detritus and phytoplankton. In Lake Kariba, *O. niloticus* may therefore prefer other more abundant prey, which may result in different effects on *Ischnura* naiads than those obtained in this study. There are also a number of other fish species, including *Pseudocrenilabrus philander*, *Pharyngochromis acuticeps*, *Tilapia rendalli* and *Tilapia sparrmanii* that occur in large numbers in inshore waters of Sanyati Basin and which probably also prey on aquatic insects and whose effect on invertebrate communities and interactions with *O. niloticus* is largely unknown.

9.4.2 Ecological significance of study results

Orechromis niloticus was first recorded in inshore waters of Lake Kariba in the early 1990s and is thus relatively new to the system. Although now abundant its effect on the trophic dynamics of Lake Kariba is largely unknown. The current study suggests that small juveniles (< 5 cm) of *O. niloticus*, which tend to be abundant in shallow vegetated margins of the eastern-most basin (Sanyati Basin) of the lake, are capable of utilizing large damsel naiads as a food source. Damsel naiads are the most abundant and dominant large insect predators associated with *Lagarosiphon ilicifolius* (Chapter 4 of this thesis). In Chapter 8, I showed that damselfly naiads may suppress the abundance of small invertebrate taxa such as planariids, glossiphonids and chironomids on *Lagarosiphon*. Removal of the damselfly naiads by fish predators resulted in significant increase in the abundances of the smaller invertebrate taxa (Chapter 8). Thus significant negative effects by *O. niloticus* on coenagrionid abundances may release smaller largely herbivorous invertebrate taxa from predation by coenagrionid naiads. Increase in abundance of herbivorous invertebrate taxa may result in increased grazing pressure and thus reduction in primary production. Trophic cascades, indirect effects of predators on the biomass of primary producers, have been observed in many systems (Brett & Goldman 1996, Schmitz *et al.* 2000, Carpenter *et al.* 2001, Halaj & Wise 2001). In Lake Kariba, there is therefore need to assess trophic dynamics, especially the effect of bottom-up (nutrients) and top-down (predation) on lake productivity.

CHAPTER 10

SUMMARY AND CONCLUSIONS

10.1 Introduction

Submerged aquatic plants are involved in a variety of essential ecosystem processes and are important components of aquatic ecosystems (Cronin *et al*. 2006). In this thesis I studied aspects of the ecology of epiphytic macroinvertebrate assemblages associated with two submerged macrophytes in shallow inshore waters of Lake Kariba. The two macrophytes, *Lagarosiphon ilicifolius* and *Vallisneria aethiopica*, are different in structural morphology. *Lagarosiphon*, which has long filiform stems with many small largely alternate leaves, offers a much more complex habitat than *Vallisneria*, which has long, basally arranged ribbon-like leaves. A key component of the thesis was to determine whether the differences in morphological complexity between the two plants affected epiphytic macroinvertebrate assemblages. I therefore assessed epiphytic macroinvertebrates associated with distinct monospecific stands of the two macrophytes at sites in shallow waters of the lake (Chapter 3). The effect of variation in habitat complexity on macroinvertebrates was also addressed with respect to variation in vegetation density of *Lagarosiphon* (Chapter 6). The thesis also dealt with aspects of the predator-prey interactions that affect epiphytic macroinvertebrate assemblages. I compared invertebrate assemblages associated with the two submerged macrophytes in experimental ponds in the absence of fish predation (Chapter 7 & 8) as well as when fish were present (Chapter 8). In Chapter 9 I explored, within small glass aquaria, the possible impacts of small (< 5 cm) juveniles of the most recent exotic fish species in Lake Kariba, *O. niloticus*, on different size classes of the damselfly *Ischnura* sp.

Epiphytic invertebrates are also affected by seasonal cycles through their influence on life-history attributes of invertebrates (Ward 1992) and macrophytes (Hargeby 1990), as well as variation in water physicochemical characteristics (Humphries 1996). *Lagarosiphon* was the dominant submerged macrophyte in the shallow marginal waters of the lake, with year-round occurrence. I therefore assessed temporal aspects of macroinvertebrate assemblages associated with *Lagarosiphon* and the effect of variation in water physicochemical parameters (Chapter 4). In Chapter 5, body size distribution, life history attributes and biomass estimates of the most common and abundant insect taxa associated with *Lagarosiphon* were assessed over a thirteen month period.

10.2 Plant Morphological Complexity and Epiphytic Macroinvertebrate Assemblages

The habitat heterogeneity hypothesis holds that due to wider range of niches, complex habitats support more diverse assemblages than simple ones (Tews *et al.* 2004). The presence of macrophytes in some areas of the littoral zone of lakes and reservoirs increases habitat structural complexity (Taniguchi *et al.* 2003) and generally results more diverse and abundant animal communities than in un-vegetated areas (Meerhoff *et al.* 2003, Teixeira-de Mello *et al*. 2009). Plant architecture (e.g. plant size and number, orientation of leaves and stems) may differ among macrophyte species, further contributing to the variation in habitat complexity (Chick & McIvor 1994).

As had been anticipated the difference in structural complexity between *Lagarosiphon* and *Vallisneria* was a key factor in structuring epiphytic macroinvertebrate assemblages associated with the two plant species in the shallow marginal waters of Lake Kariba (Chapter 3). Although the two plant species were associated with the same macroinvertebrate taxa, the average number of taxa per sample, abundances of most taxa and overall macroinvertebrate abundance were significantly greater on *Lagarosiphon*. A number of other studies have also found that the differences in macrophyte morphological complexity are to a great extent responsible for variation in the abundance of macroinvertebrates (e.g., Kershner & Lodge 1990, Cheruvelil *et al*. 2000).

The importance of plant morphological complexity in structuring invertebrate community structure was further highlighted by culturing *Lagarosiphon* and *Vallisneria* in experimental ponds (Chapters 7 & 8). When the two plant species where grown separately in fishless ponds, the number of insect taxa, diversity and total abundance were much greater on *Lagarosiphon* (Chapter 7). In contrast when the plants grew alongside each other in the same pond, only the total insect abundance was greater on *Lagarosiphon*. Thus one of the major findings was that when *Lagarosiphon* and *Vallisneria* beds occurred in close proximity, movement or exchange of insect taxa between the two plants resulted in the insect community composition being similar, although abundances were generally lower on *Vallisneria* (Chapter 7). The differences in insect assemblages on the two plants increased when the plants were spatially separated, that is cultured in separate ponds. This suggests that in the lake, extensive or large monospecific stands of *Vallineria* are possibly characterised by low epiphytic invertebrate taxa richness, diversity and abundance compared to small beds that are in close proximity or grow interspaced with *Lagarosiphon*.

During the period, 2005 to 2008, there was an apparent decline in the abundance of *Vallisneria* in shallow inshore waters of the Sanyati Basin of Lake Kariba. The decline probably had a negligible effect on epiphytic macroinvertebrates in the lake since they are no invertebrate taxa that are specific to *Vallisneria* and the abundance of most taxa generally tend to be much less on *Vallisneria* than on *Lagarosiphon*. Earlier studies by Machena (1988) and Machena & Kautsky (1988) showed that *Vallisneria* was the dominant submerged plant species in the western parts (Basin 1 and 2 see Appendix 1) of Lake Kariba, while *Lagarosiphon* dominated in the other three basins. I did not investigate the current lake-wide distribution of submerged macrophytes, but if submerged plants are distributed as was obtained in the late 1980s, Basins 1 and 2 would probably be characterised by lower overall epiphytic macroinvertebrate abundances and biomass compared to Basins 3, 4 and 5. This though needs further investigation since work done in grasslands has shown that greater plant species richness results in more efficient uptake of nutrients and greater productivity (Tilman *et al.* 1996, Symstad *et al.* 1998). Engelhardt & Ritchie (2001) also found that macrophyte diversity boosts the functioning and services such as water purification of wetland ecosystems.

10.3 Predation-prey Interactions, Plant Morphological Complexity and Macroinvertebrate Assemblages

The debate on whether ecological community structure is controlled by top-down (predation driven) or bottom-up (productivity based) trophic interactions is one of the most controversial in ecology. A number of earlier ecological studies emphasised the importance of competition for limiting resources and suggested that species coexistence, and thus community structure, largely occurs through resource partitioning (MacArthur 1972, Diamond 1978), while others (e.g., Connell 1975, Zaret 1980) considered predation to be the principal factor. The prevailing consensus is that while productivity largely determines patterns of species abundance and distribution in many ecosystems (Hunter & Price 1992), predators can also significantly influence populations and communities and under certain circumstances may prevail over bottom-up effects (Jiang & Morin 2005). It is now generally accepted that any consideration of ecological communities must include predation and environmental variability as important determinants of community structure. The coexistence by conflicting and competing species is normally enhanced by habitat heterogeneity through reduction of the intensity of biotic interactions among different species (Polis *et al.* 1989, Hampton 2004). The current study showed that variation in morphological complexity between *Lagarosiphon* and *Vallisneria* affects predator-prey interactions (Chapters 7 and 8).

10.3.1 Invertebrate predation

In Chapter 7, I studied the insect communities that developed in association with *Vallisneria* and *Lagarosiphon* in six fishless ponds. As has been found in several studies (e.g., Morin 1984a, b, Åbjörnsson *et al*. 2004) the top predatory taxa that occurred in the fishless ponds were odonates, which numerically dominated the insect assemblages in all six ponds. Unsurprisingly, only one anisopteran taxon (*Trithemis*) occurred in ponds in which *Vallisneria* was the sole plant, compared to three (*Hemicordulia*, *Diplacodes* and *Trithemis*) in ponds that had *Lagarosiphon* as the only plant. In ponds that were cultured with both plants, four anisopteran taxa, *Hemicordulia*, *Diplacodes*, *Trithemis* and *Tramea* were collected on both plants. Thus *Lagarosiphon*, with its greater morphological complexity, enabled the co-occurrence of a greater number of large insect predatory taxa than the simple morphology of *Vallisneria*. The proportional distribution of size classes of odonate taxa also differed markedly between the two plant species, especially when they occurred singly in separate ponds. In ponds that had *Lagarosiphon* a much broader range of odonate size classes was present, with similar proportions contributed to the total number of anisopteran naiads by most size-classes. The anisopteran naiads associated with *Vallisneria* were characterised by a much narrower range of size classes. Predation of large odonates on small ones is a common phenomenon (Merril & Johnson 1984, Robinson & Wellborn 1987, Fincke 1994). I explained the differences in insect assemblages between the two plants by proposing that the morphological complexity of *Lagarosiphon* reduced inter-odonate predatory interactions or intra-guild predation, which enabled the coexistence of greater numbers of predatory taxa as well as a broader range of different body sizes of naiads. Contrary, the simple morphology of *Vallisneria* could only support small numbers of a single anisoptera taxon with a narrow size class range due to enhanced predatory interactions. Finke & Denno (2002) also found that structurally complex vegetation reduced intra-guild predatory interactions between mirids and spiders, predatory invertebrates that share a common herbivorous prey. They went on to suggest that in structured vegetation multiple predator species may be more effective in suppressing herbivores, an aspect that may have important implications in the biological control of agricultural pests.

According to Benke (1976), odonates have a large daily consumption capacity, can have a standing stock that is up to three times that of their prey, and so have a numerical potential for regulating the prey community. The results obtained in Chapter 7 seem to agree with Benke's suggestions since, when fish were absent, there were very few non-predatory insect taxa associated with either *Lagarosiphon* or *Vallisneria* in all ponds, implying that the predation by the dominant odonates greatly reduced the numbers of non-predatory insects.

In Chapter 8 I investigated the impact of adding fish to three ponds that originally were fishless. Interestingly, in the pond with *Vallisneria* as the only plant, the single most dominant taxon before fish were introduced was the chironomid subfamily Chironominae, a non-predatory taxon. This finding seems to contradict the results obtained in Chapter 7, which showed numerical dominance of predatory taxa in the absence of fish predation. A possible explanation is that interactions among the predatory taxa, through intra-guild predation, facilitated the establishment of relatively large numbers of chironomids. One of the major differences between Chapters 7 and 8 in insect assemblages associated with *Vallisneria* when it occurred singly was the occurrence of greater numbers of dytiscid larvae in the latter experiment. Compared to many invertebrate predators, the role of dytiscid larvae as predators in aquatic ecosystems is not well understood (Tate & Hershey 2003). Tate & Hershey (2003), using microcosms, found that dytiscid larvae fed selectively on large mobile prey and avoided small prey. Thus it is possible that in the pond cultured with *Vallisneria* (Chapter 8) selective predation on other large invertebrate predators by relatively large numbers of dytiscid larvae resulted in a reduction of predatory pressure on chironomid larvae and so led to the establishment of greater numbers of chironomids. Thus, the predatory activities of dytiscid larvae on other large mobile predators may have had a positive indirect effect on chironomid numbers.

Another interesting observation in Chapter 8 was the occurrence of coenagrionid naiads in the ponds in which *Lagarosiphon* grew singly or together with *Vallisneria*. In the lake, coenagrionid naiads were always more abundant than anisopteran naiads (Chapters 3, 4, 5 & 6), but in the experimental ponds libellulid naiads were more abundant (Chapters 7 & 8). The numerical dominance of dragonflies in the ponds was probably due to their greater colonization ability compared to damselflies. Much more interesting was the size-class distribution of coenagrionid and libellulid naiads. Generally, a broad range of coenagrionid naiad size classes was associated with *Lagarosiphon*, while libellulid naiads were dominated by small size classes (Chapter 8, Figure 8.3). Thus coenagrionids were the main invertebrate predators in the ponds in which *Lagarosiphon* was present. Chapter 8 also illustrated the impacts of invertebrate predation, in this case coenagrionid predation, on invertebrate community structure, especially on small-bodied taxa such as chironomids. The greater the numbers of coenagrionid naiads, the greater was the negative impact on the small bodied taxa, such that on *Lagarosiphon* predation by relatively large numbers of coenagrionid naiads resulted in virtual absence of chironomids and other small-bodied taxa. The impact of coenagrionid predation was much greater on small taxa on *Lagarosiphon* than on *Vallisneria*. This finding seems to disagree with Thorp & Cothran (1984) who suggested that presence of refuges from odonates is the main factor that prevents extermination of prey species. In this case the greater refuge provided by *Lagarosiphon* compared to *Vallisneria* could not prevent the near extermination of small invertebrate taxa through predation by coenagrionid naiads. The results probably highlight the fact that predator behaviour and density may also be important in influencing prey populations.

Thus Chapters 7 & 8 illustrate aspects of macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*, and their interactions in fishless environments. The differences in morphological complexity between the two plant species are shown to affect epiphytic macroinvertebrate assemblage structure. The dominance of large and mobile invertebrate predatory taxa in the absence of fish predators is confirmed. In agreement with Peckarsky (1982) and Thorp & Cothran (1984), invertebrate predation is shown to be important in structuring macroinvertebrate assemblages. It is also observed that high densities of some invertebrate predators may overwhelm the effect of habitat complexity in providing refuge for some prey populations. The results of Chapter 8 also suggest that coenagrionid naiads, which are common and abundant on submerged vegetation in Lake Kariba, may have a strong structuring role on epiphytic assemblages of small-bodied invertebrates.

10.3.2 Fish predation

Numerous studies have shown that fish predation has significant effects on macroinvertebrate community structure and that structural complexity is important in mediating predator-prey interactions (e.g., Diehl 1992, Wellborn *et al.* 1996, Feuchtmayr *et al.* 2007)

The addition of fish to ponds that were initially without fish resulted in significant changes to invertebrate communities associated with *Lagarosiphon* and *Vallisneria* (Chapter 8). Total macroinvertebrate abundance on *Vallisneria* was drastically reduced, while fish predation had no significant effect on invertebrate abundance on *Lagarosiphon*. The result is in agreement with the finding of many studies which have shown that in the presence of fish predators, macroinvertebrate abundance tends to be more greatly impacted and reduced in structurally simple than in complex habitats (e.g., Gilinsky 1984, Diehl 1988, 1992). This is generally attributed to decrease in foraging efficiency by fish in highly heterogeneous habitats such as those afforded by dense beds of morphologically complex macrophytes (Dibble *et al*. 1996, Swisher *et al.* 1998).

Chapter 8 also showed that in the absence of fish predators the epiphytic macroinvertebrate community on both *Lagarosiphon* and *Vallisneria* was dominated by relatively large and mobile predatory taxa. As already mentioned, adding fish predators drastically reduced total macroinvertebrate abundance associated with *Vallisneria*. In the pond where *Vallisneria* was the only plant, the abundance of oligochaetes increased, while in the pond where it grew alongside *Lagarosiphon*, planariid numbers also increased after fish were added. On *Lagarosiphon* there was a sharp and distinct increase in the abundance of Chironominae after fish were added, with the other relatively small taxa such as planariids and oligochaetes also becoming more abundant and frequent, while coenagrionid naiads were eliminated. The results imply that in the absence of fish predation, large predatory invertebrates suppressed the abundance of small taxa on both *Lagarosiphon* and *Vallisneria*. Fish predation on large predatory invertebrates, especially with respect to invertebrates associated with *Lagarosiphon*, reduced the abundance of invertebrate predators and so led to increased abundances of small taxa, especially non-predatory chironomids. Other studies (e.g., Gilinsky 1984, Batzer *et al.* 2000) have shown that in heterogeneous environments size-selective fish predation on invertebrates may have indirect positive effects on small invertebrate taxa, by freeing them from predation by other invertebrate taxa.

The results from Chapter 8 also showed that with respect to macroinvertebrates associated with *Lagarosiphon*, fish predation primarily affected the larger coenagrionid naiads and had no effect on the more abundant but smaller libellulid naiads. The abundance of the smaller libellulid naiads on *Lagarosiphon* actually increased after fish were introduced to the ponds. Concomitant with the removal of coenagrionid naiads was an increase in chironomid larval abundance on *Lagarosiphon*. Thus size-selective fish predation affected the body-size structure of the macroinvertebrate community. The findings of the study suggest that chironomid abundances on *Lagarosiphon,* as well as those of other small invertebrate taxa, were low before fish were added, primarily due to predation by coenagrionid naiads.

Chapter 8 also raised the possibility of trophic cascades due to fish predation on macroinvertebrates associated with submerged vegetation in Lake Kariba. A trophic cascade is a strong effect imposed by top predators on their prey biomass, which cascades down to plants in a food chain and plays an important role in determining the overall structure of the community (Hall *et al.* 2007). Although a controversial concept, trophic cascades have been reported from both terrestrial (e.g., Schmitz *et al.* 2000, Halaj & Wise 2001) and aquatic ecosystems (e.g., Carpenter *et al*. 2001). In Chapter 8 the elimination of large invertebrate predators and increase in the abundances of small largely non-predatory invertebrates that occurred after adding fish, possibly resulted in increased grazing pressure on primary producers such as algae. Carpenter *et al.*, (1987, 2001) showed that fish predation on predatory invertebrates reduced predation pressure on invertebrate grazers and resulted in increased biomass of primary producers. Most studies on trophic cascades in aquatic ecosystems have been reported from temperate regions, largely in pelagic zones of lakes and reservoirs. This study suggests that trophic cascades may also occur through the benthic food-web. According to Lazzaro (1997) high abundances of omnivorous fish species in the littoral zone of tropical and subtropical lakes and reservoirs may have different effects on lower trophic levels than those predicted by the trophic cascade theory. The effect of fish predation on lower trophic levels in Lake Kariba requires further investigation.

As has been observed in other tropical and subtropical water bodies (e.g., Meschiatti *et al*. 2000, Teixeira-De Mello *et al.* 2009), small fish (i.e. juveniles and many small-bodied fish species) occur in large numbers within macrophyte beds in shallow inshore waters of Lake Kariba. In the Sanyati Basin of Lake Kariba, *O. niloticus* juveniles are among the most abundant fish in inshore waters. In Chapter 9 I explored, within small glass aquaria, the effect of *O. niloticus* juveniles whose body size was less than 5 cm on damsel (*Ischnura* sp.) naiads in moderate-density beds of *Lagarosiphon*. Studies done in East Africa on Lake Victoria found that insects constituted an insignificant proportion to the diet of small (< 5 cm) juvenile *O. niloticus* but were a key component of larger fish (Njiru *et al.* 2004). This was attributed to the small mouth gapes of the small fish, which restricted them to small prey items such as zooplankton. The results of the current study showed that small (< 5 cm) *O. niloticus* can consume insects and actually preferred the large sizes (length > 10 mm) of damselfly naiads over small (length < 5 mm) and moderate (5 – 10 mm) sizes. Generally, even at low fish density, short-term (24-hour) survival of large naiads was low (≤ 10%). Interestingly, moderate sizes were the least susceptible to fish predation with their short-term survival significantly affected at a much higher fish density of about 200 m^{-2} compared to 60 m^{-2} for small-bodied naiads. The much lower survival of small sizes compared to moderate sizes of naiads was attributed to interactions among the naiads (e.g., cannibalism) that probably resulted in small sizes being more active and so more vulnerable to fish predation than to moderate sizes. The study suggests that in moderate-density beds of *Lagarosiphon*, low densities of juvenile *O.niloticus* affect coenagrionid naiads largely through size-selective predation on large individuals. The level of impact on small and moderate-sized coenagrionids increased with increase in fish density.

Thus overall, Chapters 7, 8 and 9 showed that fish predation has a significant effect on epiphytic macroinvertebrate communities associated with *Lagarosiphon* and *Vallisneria*. Comparatively, its impact is much greater on *Vallisneria* than on *Lagarosiphon*, which results in significantly less total macroinvertebrate abundance on *Vallisneria* compared to *Lagarosiphon.* On *Lagarosiphon*, size-selective predation on, and eventual removal of, coenagrionid naiads resulted in significant increase in small-bodied invertebrate taxa, especially non-predatory chironomids, implying that fish predation has considerable direct and indirect impacts on macroinvertebrate assemblages. The results suggest that predatory fish have considerable impacts on lower trophic levels.

10.4 Temporal Aspects of Macroinvertebrates Associated with *Lagarosiphon*

Temporal attributes of communities are essential in ecological investigations and according to Wiens *et al*. (1986) ecological studies that are limited in temporal scale may fail to unravel the pertinent processes structuring communities. Physicochemical environmental variables, such as pH, temperature and oxygen concentration, are important in physiological processes of invertebrates and so in structuring macroinvertebrate assemblages. Therefore temporal and spatial variation in physicochemical environmental conditions can lead to differences in macroinvertebrate community structure (e.g., Mykä 2006). Differences in life-history cycles also result in temporal variation in macroinvertebrate assemblages (e.g., Oertli 1995).

10.4.1 Temporal variation in macroinvertebrate abundance on *Lagarosiphon*

In Chapter 4 I investigated the temporal variation in macroinvertebrate assemblages associated with *Lagarosiphon* in Lake Kariba over a thirteen-month period. I also assessed the importance of some physicochemical variables in structuring the epiphytic macroinvertebrates on *Lagarosiphon*. Of a total of 86 taxa, the sixteen most common, which were *Dugesia* sp, Oligochaeta, *Physa acuta*, Hydracarina, *Cyclestheria hislopi*, Ostracoda, *Caenis* sp, *Cloeon* sp, *Pseudagrion* sp, *Enallagma* sp, *Ischnura* sp, *Micronecta* sp, *Orthotrichia* sp, Chironominae, Tanypodinae and Orthocladiinae, made up more than 95% of the total number of organisms. Although significant temporal differences occurred in the abundance of individual taxa, there were considerable similarities (>60%) in macroinvertebrate assemblage composition among months. The relative high similarities of macroinvertebrate communities obtained over the thirteen months suggest that physicochemical conditions did not change enough during the study period so as to dramatically affect macroinvertebrate assemblage composition. The year-round occurrence of most taxa also suggests that the macroinvertebrates are probably ecological generalists, able to survive under most of the conditions that occurred during the study period.

10.4.2 Effect of temperature and water-level fluctuation

Irrespective of lack of significant temporal variation in macroinvertebrate assemblage composition on *Lagarosiphon*, it was noted in Chapters 4 and 5 that water temperature and water-level fluctuation may be critical in macroinvertebrate productivity. Water temperatures in the upper 20^{O}Cs and lower 30^{O}Cs were characterised by decrease in the abundance of some macroinvertebrate taxa and overall macroinvertebrate abundance, while the abundances of a number of taxa were positively correlated with water level. The results obtained in Chapter 4 suggest that from November to April, when abundances were consistently low (Figure 4.4), thermal conditions (>28^{O}C) may have been sub-optimal for hatching of eggs, growth and reproduction for most macroinvertebrate taxa. The upper thermal tolerance limits of ectotherms are generally similar at global scales (Chown & Gaston 2008) and according to Compton *et al.* (2007) and Deutsch *et al*. (2008), ectotherms from warm climates are currently living close to their optimal temperatures and thus are much more sensitive to increase in temperature than those from temperate climates. The effect of water temperature on invertebrate assemblages of Lake Kariba was therefore identified as urgently requiring further investigation.

In Chapter 5 it was shown that most of the six common insect taxa have multivoltine life cycles, with biomasses of most taxa, and total insect biomass, positively correlated with water level. Water level fluctuation in lakes has been shown to affect both macrophytes (e.g., Hellsten 2001) and macroinvertebrates (e.g., Aroviita & Hämäläinen 2008). The findings of Chapters 4 and 5 have critical implications, especially when considered together with the predictions of global climate change, which generally suggest an increase in temperatures over much of Africa (Hulme *et al*.

2001) and significant reductions in water flow on the Zambezi River (Harrison & Whittington 2002). These changes are likely to result in reduced abundances, biomass and production of macroinvertebrates in the inshore water of Lake Kariba.

10.5 Other Notable Observations of the Study

A number of other interesting observations were made in this study. I assessed the relationship between variations in *Lagarosiphon* density with epiphytic macroinvertebrate assemblage structure (Chapter 6). The macroinvertebrate composition, abundance and diversity did not vary among low-, moderate- and high-density beds. I had expected that through fish predation, whose influence is generally much reduced in complex habitats, invertebrate abundance and diversity would increase with increase in the density coverage of *Lagarosiphon*. The macroinvertebrate communities across the density gradient were dominated by small-bodied taxa, including ostracods, *C. hislopi*, Chironominae and oligochaetes. I proposed that the lack of a distinct pattern in macroinvertebrate assemblage and the dominance of small-sized taxa were probably due to high and relatively uniform fish predation across the vegetation-density gradient. The analysis of body size class distribution of the mayfly *Cloeon* showed, however that large individuals were absent from low-density but present in moderate- and high-density vegetation beds. This was probably due to greater predation pressure by fish in low- than in moderate- and high-density beds. Contrary to the size-class distribution observed for *Cloeon*, large-sized coenagrionid naiads occurred in low- and moderate- but were absent from high-density beds. This was probably because large-bodied coenagrionid naiads chose low and moderate vegetation density beds because of greater foraging success in these than in high-density beds. Thus although macroinvertebrate assemblage composition, taxon richness and diversity did not vary across the vegetation density gradient, the study suggest that body size-class distributions of predatory and non-predatory taxa can be influenced by variation in vegetation density. This agrees with a number of findings which have suggested that habitat complexity can influence predator-prey interactions (e.g., Hampton 2004).

In general, beds of all degrees of vegetation density were dominated by small non-predatory invertebrate taxa, with the abundance of large predatory invertebrates much reduced. This was probably due to size selective predation by fish. These findings agree with those obtained in Chapters 7, 8 and 9. In Chapters 7 and 8 invertebrate communities associated with *Lagarosiphon* in experimental ponds were dominated by large invertebrate predators in the absence of fish predation but by small non-predatory taxa in the presence of fish predators. Chapter 9 demonstrated that large damsel naiads are more susceptible to fish predation than small and moderate-sized ones.

10.6 Management Implications

An understanding of the relationship between macrophytes and macroinvertebrates is important for the management of aquatic ecosystems. In Lake Kariba, *Lagarosiphon ilicifolius* is the dominant submerged macrophyte, while *Vallisneria aethiopica* is common and widespread (Machena & Kautsky 1988). The two macrophytes are therefore important in sustaining the productivity of the lake, notably in maintaining inshore fish communities, through the provision of cover and food sources. This study has shown that differences in structural complexity between *Lagarosiphon* and *Vallisneria* affect epiphytic macroinvertebrate abundance. The findings of the study also suggested that fish predation affects epiphytic macroinvertebrate composition and abundance. An inference of the study is that differences in structurally complexity of the two macrophytes also affect inshore fish productivity. Conservation and management of inshore fish communities of Lake Kariba must therefore include ensuring the presence of healthy populations of submerged macrophytes.

The study showed that temperature and water level fluctuations are important in structuring macroinvertebrate associated with *Lagarosiphon*, affecting the abundances of a number of taxa and the total biomass of aquatic insects. Conservation and management of inshore fish communities on Lake Kariba therefore need to incorporate the potential effects of global climate change on temperature and water level fluctuations. There is need for further studies that will enhance our understanding of the relationships among temperature, water fluctuations, invertebrates and fish communities in the lake.

The findings of the study are also important for the possible utilization of epiphytic macroinvertebrates in biomonitoring of water quality in shallow waters of the lake. The main macroinvertebrate taxa associated with *Lagarosiphon* were present all year round, and variation in vegetation density coverage did not significantly affect the composition of macroinvertebrates on *Lagarosiphon*. This suggests that seasonal variation in macroinvertebrate assemblages and vegetation density may not be key aspects when undertaking biomonitoring surveys using epiphytic macroinvertebrates associated with *Lagarosiphon*.

10.7 Conclusions

The major findings of the study are:

1. The macroinvertebrate assemblages associated with *Lagarosiphon* and V*allisneria* in shallow marginal waters of Lake Kariba were characterised by similar taxonomic composition. The abundance of most of taxa and total macroinvertebrate abundance was greater on *Lagarosiphon*, due its greater structural complexity, than on *Vallisneria*.
2. The taxonomic composition of the macroinvertebrate assemblage on *Lagarosiphon* was generally similar over a period of thirteen months, although there were significant temporal differences in the abundances of some of the taxa. The temporal differences in macroinvertebrate community structure were largely due to variations in temperature and water level fluctuations. High water temperature (> 28^{O}C) had an adverse effect on the abundances of a number of taxa and total macroinvertebrate abundance. Water level fluctuation affected total biomass of the aquatic insects on *Lagarosiphon*.
3. Variation in density of *Lagarosiphon* had no effect on water physicochemical variables and epiphytic macroinvertebrates abundance, richness and diversity. Vegetation density, through its mediatory role in predator-prey interactions, affected the body size distribution of the mayfly *Cloeon* and coenagrionid naiads.

4. Fish predation affects macroinvertebrate assemblages associated with *Lagarosiphon* and *Vallisneria*.

10.8 Suggestions for Future Research on Lake Kariba

1. *An assessment of the effect of temperature on macroinvertebrate assemblages in inshore waters*

   The current study showed that the abundance of a number of taxa as well as total macroinvertebrate abundance on *Lagarosiphon* generally decreased at water temperatures that were greater than 28^{O}C. This suggests that thermal conditions may be sub-optimal for a number of invertebrates in Lake Kariba once temperatures get above 28^{O}C. It is therefore essential to assess in greater detail the response of the major invertebrate taxa to variation in temperature, especially considering that over the coming decades mean temperatures are predicted to rise due to global climate change.
2. *Further quantitative assessments of the effect of fish predation on macroinvertebrate communities in the littoral zone of Lake Kariba*

   In this study I experimentally assessed the effects of fish predation on macroinvertebrates associated with *Lagarosiphon* and *Vallisneria* using small ponds and glass aquaria. Field-based studies, such as exclusion experiments, on Lake Kariba are needed if greater understanding of the ecosystem is to be attained.
3. *Comparative studies of the macroinvertebrates of bottom sediments, submerged plants and floating plants* (*Eichhornia crassipes*)

   A comprehensive understanding of macroinvertebrate assemblages in Lake Kariba requires studies on benthic macroinvertebrates as well as the assemblages on other common aquatic macrophytes.
4. *Detailed taxonomic studies of aquatic macroinvertebrates*

   Very little is known about invertebrate biodiversity in Lake Kariba.
5. *Using macrophytes and the associated macroinvertebrates for monitoring aquatic ecosystem health*

Human activities have negatively affected freshwater ecosystems, largely through physical alteration, habitat loss and degradation, water withdrawal, overexploitation, pollution, and the introduction of non-native species (Revenga *et al.* 2000, Revenga & Kura 2003, Ellison 2004). Freshwater systems are now more threatened than terrestrial ecosystems (Revenga *et al*. 2005). The development of management and conservation tools for freshwater ecosystems is therefore critical. Biological monitoring systems that use macrophytes, macroinvertebrates as well as other organisms are therefore important complements to conventional physicochemical assessment of water resources. Sampling for macrophytes and macroinvertebrates generally is easier than other organisms such as fish and bacteria. Developing and use of biomonitoring tools requires knowledge of the ecology of target organisms to be used in assessing freshwater ecosystem health. This study will hopefully aid the process of developing biomonitoring tools on Lake Kariba.

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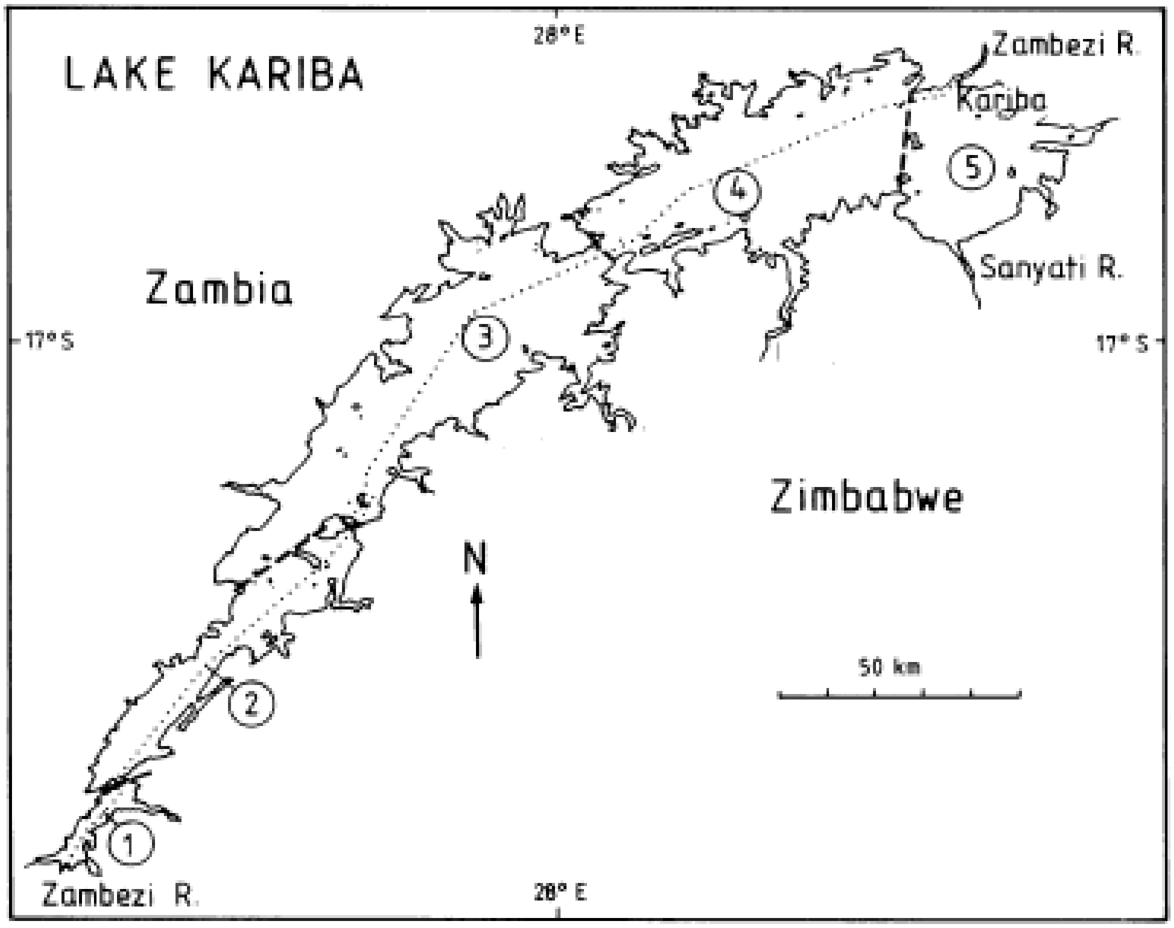
Appendix 1. Lake Kariba showing the five main hydrological basins (1-5).



Appendix 2. Sampling sites characterised based on notable human activities with 500m of the shoreline of Sanyati Basin.

SITE	1	2	3	4	5	6	7	8	9	10
Co-ordinates										
Activity										
Residential area	0	0	0	0	0	0	0	3	1	1
Commercial Aquaculture activities	0	0	0	3	0	3	0	2	0	0
Maintenance of boats & boating activities	0	0	0	2	3	1	3	2	3	2
Hotel/lodges/chalets	0	0	0	0	0	1	2	0	1	0
Road and Vehicle density	0	0	0	3	2	2	3	3	3	2
Urban Development	0	0	0	2	2	2	3	3	3	2
Industrial Development	0	0	0	1	3	0	1	3	3	1
Active construction activities	0	0	0	3	3	0	0	3	3	2
Sewage effluent disposal	0	0	0	0	0	3	0	0	0	0
Effluent disposal from farming activities	0	0	0	3	0	2	0	0	0	0
Domestic human activities (washing)	0	0	0	0	0	0	0	3	0	0
Total disturbance Score [a]	0	0	0	17	13	14	12	22	17	10
Disturbance Category [b]	N	N	N	M	M	M	M	M	M	L

[a] Overall disturbance score used for categorizing each site into one of four categories: 0, no evident disturbance; 1–11, little disturbance;12–22, moderate disturbance; 23–33,much disturbance
[b] The human disturbance category within which each site fell is represented by N = none or no disturbance, L = low, M = medium and H = high

Appendix 3: Results of water physical and chemical variables measured at the ten sites in shallow marginal waters of Sanyati Basin between May and July 2005.

Month	Site	Temp (^{O}C)	DO (mg/L)	DO (%sat)	Cond (μScm^{-1})	pH	Turbidity (NTU)	NH_4^+ (μg/L)	NO_3^- (μg/L)	PO_4^{3-} (μg/L)	TP (μg/L)
May	1	26	4.9	62.8	102.5	7.36	15	62.7	42.8	1.8	1.8
July	1	24.9	5.6	72.2	99.8	8.01	18				
May	2	28.3	5.5	70.7	98.4	8.18	5	25	27.6	21.1	1.4
July	2	26.5	6.0	76.9	100	8.33	3.7				
May	3	27.2	5.0	63.8	98.3	8.81	10	24.2	32.6	12.6	2.9
June	3	26.3			94.8	8.5	6.01	39.2	10.7	2.1	22
July	3	24.6	5.6	71.6	94	8.35	6				
May	4	24.8	3.9	49.8	96.4	5.98	11.5	76.7	62.8	52	16.1
June	4	25.2			96.6	8.08	20.1	20.3	12.2	5.8	37.2
July	4	24.6	4.1	52.1	104.5	7.04	15.2				
May	5	25.7	4.3	55.0	97.1	6.47	17	19.9	30.2	0.6	3.1
June	5	22.4			97.4	6.27	10.5	17.7	23.2	4.8	20.1
July	5	25.1	5.3	67.8	95.5	7.26	5.2				
May	6	28	4.7	59.7	94.2	8.61	35	31.5	37	6.4	11.3
June	6	25.5			95.8	8.55	11.1	30.1	8.6	2.1	18.5
July	6	22.2	5	64.0	96.1	7.44	12				
May	7	27.2	3.9	49.9	97.5	6.98	5	28	36.4	1	17.7
June	7	25.9			98.1	7.16	7	35.3	8.6	3.7	19.4
July	7	25.5	4.6	58.8	98.8	7.21	12				
May	8	26.6	4.3	54.9	96.4	7.44	2	16	28	21.5	5.3
June	8	24.9			97.8	7.31	2.2	27.1	12.6	0	13
May	9	27.6	4.4	56.0	96.4	7.1	6	17.1	31.5	1.8	13.8
June	9	23.4			97.7	6.31	3	24.2	10.1	13.7	16.5
July	9	25	5.4	69.3	95.5	7.5	8.3				
May	10	26.8	3.9	49.8	94.7	6.91	11	15.2	24.1	2.1	0.1
June	10	24.5			95.4	7.37	3.1	9.2	8.1	3.7	7.8
July	10	23.8	5	63.7	95.1	7.28	2.8				

APPENDIX 4:

Phiri C., Day J., Chimbari M. and Dhlomo E. 2007. Epiphytic diatoms associated with a submerged macrophyte, *Vallisneria aethiopica***, in the shallow marginal areas of Sanyati Basin (Lake Kariba): a preliminary assessment of their use as biomonitoring tools**

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ORIGINAL PAPER

Epiphytic diatoms associated with a submerged macrophyte, *Vallisneria aethiopica*, in the shallow marginal areas of Sanyati Basin (Lake Kariba): a preliminary assessment of their use as biomonitoring tools

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Abstract Diatom assemblages attached to the leaves of the submerged macrophyte *Vallisneria aethiopica* in the shallow waters of the Sanyati Basin in Lake Kariba were analysed to assess their response to human impact. Human activities occurring within approximately 500 m of the shoreline were assessed at ten sampling sites along the shores of the basin. Eleven human activity factors were assessed and scored on a scale of 0 (not occurring at the site), 1 (low), 2 (medium) and 3 (high). Based on these 11 factors, we obtained a total score for the sites, which were then categorized as either having no human disturbance (0), low human disturbance (1–11), medium human disturbance (12–22) or high levels of human disturbance (23–33). Three sites were categorized as having no human disturbance, one had low disturbance and six had medium level human disturbance. A total of 9993 diatoms belonging to 40 genera were identified. The most abundant genera were *Achnanthidium* and *Gomphonema*, which made up 23.4 and 42.9% of the total diatom count, respectively. *Achnanthidium* dominated in remote areas with minimal human activities, while *Gomphonema* was more abundant in areas adjacent to increased human activities. The relative abundances of *Achnanthidium*, *Denticula*, *Pinnularia*, *Rhopalodia* and *Stauroneis* were negatively and significantly correlated, while that of *Gomphonema* was positively and significantly correlated to the human disturbance score (Spearman correlation, $P < 0.05$). Although the number of genera, the Shannon Diversity Index and evenness did not differ significantly among sites (ANOVA, $P > 0.05$), the lowest levels of these descriptors of community assemblage occurred at sites located near areas with relatively high human activities. The abundances of *Achnanthes*, *Cymbella*, *Denticula*, *Encyonema* and *Pinnularia*, *Bacillaria* and *Mastogloia*, *Diatoma* and *Navicula* and *Eunotia* and *Mastogloia* significantly decreased with increasing levels of total phosphorous, nitrate–nitrogen (N), ammonium–N and water turbidity, respectively (Spearman correlation, $P < 0.05$). Of the16 diatom index of biotic integrity (DIBI) metrics, 11 were significantly correlated with at least one of the environmental variables, while nine metrics were significantly correlated with the composite DIBI. Among the environmental variables the disturbance score was the only one that was significantly correlated with the DIBI. We conclude that although there is need for further work,

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periphytic diatoms associated with *V. aethiopica* may potentially be useful in assessing ecological conditions or the impact of human activities within the shallow marginal waters of Lake Kariba.

Keywords Biomonitoring · Diatoms · Disturbance · Sanyati Basin · Submerged macrophyte

Introduction

Widespread anthropogenic pressures on aquatic ecosystems caused by rapid urbanization, industrial expansion and agricultural activities have resulted in increased loads of inorganic and organic materials and, consequently, adverse effects on aquatic environments. Water quality assessment is principally a biological problem in that its primary effect is on living organisms (Gaufin 1973). The quality of water is generally reflected in the indigenous communities of aquatic organisms in terms of the composition and diversity of the species present, their population densities and their physiological condition(Weber 1973). Although over the last few decades a number of biological monitoring methods have been developed for the assessment of the condition of freshwater environments, these have rarely been applied in Africa. In the few African countries where regular monitoring of the quality of the aquatic environment is practiced, the tendency has been to concentrate on physical and chemical water quality determinants.

Diatoms (Class Bacillariophyceae) are abundant in almost all aquatic habitats, constituting an estimated 25% of the Earth's primary production (Werner 1977). They are increasingly being used to assess water quality as they are generally species-rich, relatively easy to sample, have quick responses to changes in physical and chemical characteristics and are sensitive to subtle changes in environmental conditions or disturbances that may affect other communities only at greater levels of disturbance (e.g., Dixit et al. 1992; Bahls 1993; Lowe and Pan 1996; Stevenson and Bahls 1999). A number of studies have shown that diatoms are excellent biological indicators for many types of pollution in aquatic systems (Patrick and Palavage 1994; Kelly et al. 1995). However, the use of diatoms in water quality programs in African countries has been limited largely due to a dearth of basic phycological research.

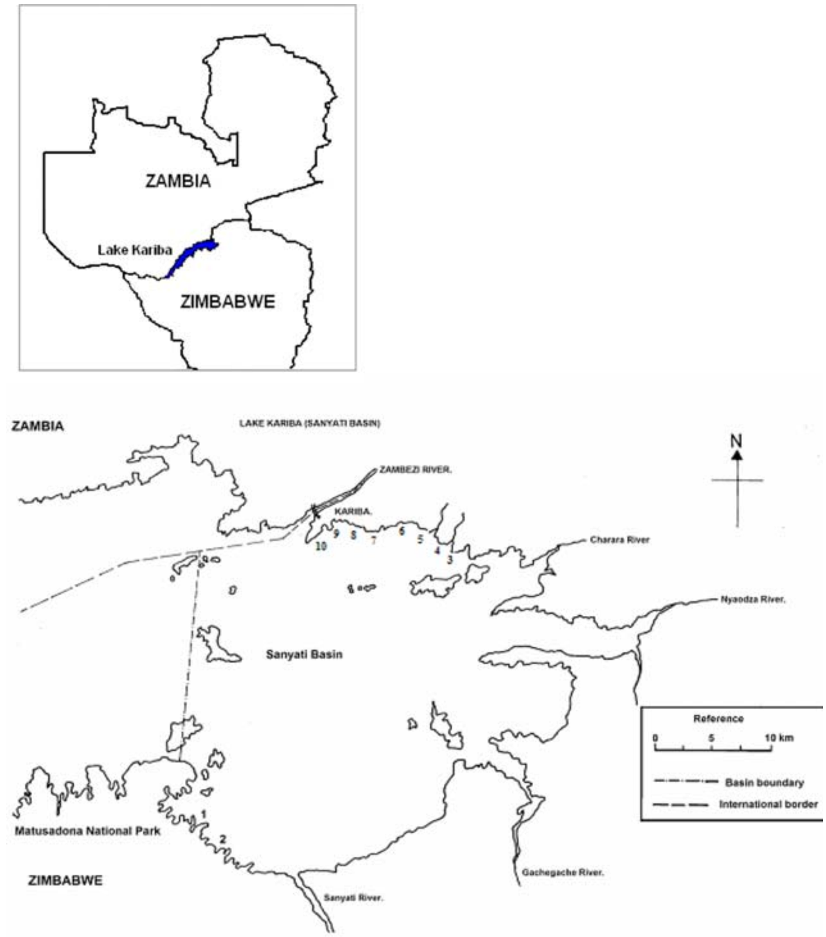
Lake Kariba is a large, minimally polluted and oligotrophic man-made lake, although some areas presently are becoming polluted by increased human activities along its shores. The objective of this study was to determine the response of the periphytic diatom community associated with *Vallisneria aethiopica*, which was the most common and dominant submerged macrophyte during the study period, to human activities or impacts along the shores. It is part of a more comprehensive study aimed at developing a suite of biotic indicators for the assessment of ecological integrity in the shallow zones of Lake Kariba using diatoms and macroinvertebrates.

Materials and methods

Lake Kariba was formed in 1958 by the damming of the Zambezi River. The Zambezi River, with a catchment area of about 1,193,500 km^2, is southern Africa's largest river and is composed of three ecologically distinct zones, the Upper (1078 km), Middle (853 km) and Lower Zambezi (563 km). Lake Kariba lies within the Middle Zambezi zone, between latitudes 16°28′ S and 18°06′ S, and longitudes 26°40′ E and 29°03′ E. The lake has a surface area of 4364 km^2 at the normal operation level of 484 m a.s.I, a length of 276 km, an average width of 19 km and an average depth of 29 m. The lake is shared between Zambia and Zimbabwe and has over the years developed a variety of other uses, such as tourism, aquaculture and inshore and pelagic fishery industries.

The study was carried out in the Sanyati Basin of Lake Kariba (Fig. 1), the easternmost of the five major basins forming the lake. For the purposes of the study, the shoreline was divided into areas with minimal human activities, peri-urban areas and urban areas. The areas of minimal disturbance are located in the southern part of the basin adjacent to Matusadona National Park. Ten sites were selected from these areas in a targeted manner to cover the full range

Fig. 1 The location of sampling sites (*1–10*) along the shoreline of the Sanyati Basin of Lake Kariba. *Insert* The location of Lake Kariba between Zambia and Zimbabwe



of human impacts known to occur along the shores of the basin. Water and periphytic diatom samples were collected monthly at the ten sites between May and July of 2005.

Notable human activities or developments within 500 m of the shoreline include residential areas, commercial aquacultural activities, maintenance of boats and boating activities, hotels and other tourist accommodation, roads and vehicles, urban development, industrial development, construction activities, sewage effluent disposal, domestic activities (washing and bathing) and effluent disposal from farming activities. To estimate relative degrees of disturbance among the sites, we scored the level of impact of each activity or development at each site qualitatively on a scale of 0 (not occurring at the site) through 1 (low) and 2 (medium) to 3 (high). An overall total human disturbance score was thus obtained, and each site was subsequently categorized as belonging to one of four categories: no evident disturbance (0), little disturbance (1–11), moderate disturbance (12–22) and much disturbance (23–33).

Five water samples (2-l bottles) were collected at each sampling site from different points along a stretch of about 100 m. All samples from each site were put into a 20-l bucket from which a 2-l sub-sample was taken for analysis of the concentrations of ammonium, nitrates, phosphates, total phosphorus (P) and sulphates. Water temperature, pH, dissolved oxygen, conductivity and turbidity were measured in situ. Temperature, pH and dissolved oxygen were measured with a mercury thermometer, a WTW 330i pH meter (Geotech Environmental Equipment, Denver, Colo.) and WTW Oxi 330 oxygen meter (Geotech Environmental Equipment), respectively.

The concentrations of ammonium, nitrates, phosphates, total P and sulphates were obtained using the spectrophotometric methods described by Madera et al. (1982). Analysis of variance (ANOVA) was used to test for differences between sites in the physical and chemical variables measured.

To sample for epiphytic diatoms, five plants of the submerged macrophyte *Vallisneria aethiopica* were randomly chosen from different points along a stretch of about 100 m at each site. The plants were cut underwater with scissors and gently brought to the surface, taking care not to disturb the biofilm on the plants. Three portions of leaf were obtained from each plant. The diatoms were separated from the leaf fragments by vigorously shaking the fragments for 1 min in 1-l of tap water and then lightly scraping each segment using a toothbrush after which a 100 ml sub-sample was preserved in Lugol's solution. In the laboratory, diatom valves were prepared for light microscopy using acid cleaning following the procedures of Biggs and Kilroy (2000). Two permanent Naphrax slide mounts were prepared for each sample. Diatoms were viewed under at a magnification of 1000× using immersion oil. A minimum of 300 diatom valves was counted from one of the slides prepared from each site. The diatoms were identified to the genus level using standard taxonomic texts.

The number of diatom genera obtained in each sample was recorded. The percentage relative abundance of each taxon in each sample was calculated as

$$\text{Relative abundance } \% = (n_i/N) * 100$$

where n_i refers to the number of individuals of taxa i in the sample, and N refers to the total number of diatoms counted in the sample. Spearman rank correlations were evaluated using STATISTICA ver. 7 (StatSoft 2004) to determine the relationship between diatom abundance, human disturbance and water physical and chemical variables.

Diatom community diversity was calculated for each sample as Shannon's Diversity Index H' (Shannon and Weaver 1949). The mathematical equation for the Shannon-Wiener index is

$$H' = -\Sigma^S n_i/n \ln n_i/n$$

where H' is the community diversity, n is the total number of organisms in the sample, n_i is the number of individuals per taxon and S is the total number of taxa counted per sample.

An evenness index, the Pielou index (Krebs 1989; Clarke and Warwick 1994), was calculated for each sample using the formula

$$J' = H'/\text{Log } S$$

in which H' is the Shannon-Wiener function and S refers to the number of taxa counted per sample. Kruskal-Wallis ANOVA was used to test for differences in diversity and evenness between sites. Spearman rank correlations were evaluated to determine the relationship (if any) that existed between the number of genera per site and the diversity and evenness indices and human disturbance and water physical and chemical variables.

We also calculated 16 diatom index of biotic integrity (DIBI) metrics using the environmental preferences of diatom species taken from published literature (van Dam et al. 1994; Hill et al. 2000) (Table 1). The mean environmental ratings for species within a genus were used as the environmental preferences of the diatom genera. The metrics were scored from 0 to 10, with decreasing scores corresponding to increasing human disturbance. The DIBI for each sample was determined by calculating the sum of the 16 metrics. The individual metrics and the total DIBI were then evaluated against human disturbance scores and water physical and chemical variables using the Spearman correlation.

Results

None of the sites was categorized as being highly disturbed (Table 2). Sites 1, 2 and 3 were categorized as having no human disturbance; Site 10 had a low human disturbance score, and the other six sites were moderately disturbed. The highest human disturbance score was obtained for Site 8 (Table 2).

The mean values for the physical and chemical variables at the ten sites are shown in Table 3.

Table 1 The metrics included in the diatom index of biotic integrity (DIBI)

Metric	Ecological indicator values[a]	Calculation	Range	Score[b]
Relative taxa richness metric		Number of algal genera/ expected no. algal genera[d]	0–1	0–10
Dominant diatom metric		1–(No. dominant diatoms/total no. diatoms)	0–1	0–10
Motile diatoms metric[c]		1–(No. motile diatoms/total no. diatoms)	0–1	0–10
Acidophilic diatom metric	Mainly occurring at pH < 7	1–(No. acidophilic diatoms/total no. diatoms)	0–1	0–10
Circumneutral diatom metric	Mainly occurring at pH values about 7	1–(No. circumneutral diatoms/ total no. diatoms)	0–1	0–10
Alkaliphilic diatom metric	Mainly occurring at pH > 7	1–(No. alkaliphilic diatoms/total no. diatoms)	0–1	0–10
Nitrogen-autotrophic diatom 1 metric 1 (–1)	Tolerating very small concentrations of organically bound nitrogen	1–(No. nitrogen-autophic diatoms 1/total no. diatoms)	0–1	0–10
Nitrogen-autotrophic diatom metric 2 (–2)	Tolerating elevated concentrations of organically bound nitrogen	1–[No. nitrogen-autophic (–2) diatoms/total no. diatoms]	0–1	0–10
Oxygen requirement 1 metric	Continuously high oxygen requirements (about 100% saturation)	1–(No. diatoms with continuously oxygen requirements/total no. diatoms)	0–1	0–10
Oxygen requirement 2 metric	Fairly high oxygen requirements (above 75% saturation)	1–(No. diatoms with fairly high oxygen requirements/total no. diatoms)	0–1	0–10
Oxygen requirement 3 metric	Moderate oxygen requirements (above 50% saturation)	1–(No. diatoms with moderate oxygen requirements/total no. diatoms)	0–1	0–10
Oxygen requirement 4 metric	Low oxygen requirements (above 30% saturation)	1–(No. diatoms with low oxygen requirements/total no. diatoms)	0–1	0–10
Oligo-mesotraphentic diatoms metric		1–(No. oligo-mesotraphentic diatoms/total no. diatoms)	0–1	0–10
Mesotraphentic diatoms metric		1–(No. mesotraphentic diatoms/ total no. diatoms)	0–1	0–10
Meso-eutraphentic diatoms metric		1–(No. meso-eutraphentic diatoms/total no. diatoms)	0–1	0–10
Eutraphentic diatoms metric		1–(No. meso-eutraphentic diatoms/total no. diatoms)	0–1	0–10
			0–1	0–10
Range of potential DIBI scores				0–160

[a] The ecological indicator values were obtained from van Dam et al. (1994)

[b] Score range was obtained by multiplying the raw range by 10

[c] Motile diatom genera classification obtained from Hill et al. (2000)

[d] The expected number of genera was the observed maximum number of genera for each month

The only variables that differed significantly between the sites were pH and turbidity. The mean pH at Sites 2, 3 and 6 was significantly greater than that at Sites 4, 5, 7, 9 and 10, with the pH at Site 3 also being significantly greater than that of Site 8 (ANOVA, $F_{9,17} = 4.03$, $P < 0.05$). The turbidity at Site 2 was significantly greater than that at Sites 4 and 5, while that of Site 6 was significantly greater than that at Sites 3, 7, 8, 9 and 10 (ANOVA, $F_{9,17} = 2.55$, $P < 0.05$).

A total of 9993 diatoms were counted and 40 genera identified (Table 4). Nine genera, *Achnanthidium*, *Cocconeis*, *Diatoma*, *Encyonema*, *Fragilaria*, *Gomphonema*, *Navicula*, *Nitzschia*, and *Synedra* occurred at all ten sites. The two most abundant genera were *Achnanthidium* and *Gomphonema*, which comprised 23.4 and 42.9% of the total number of diatoms counted, respectively. *Achnanthidium* was most abundant at Sites 1 and 3, making up 63.1 and 41.1%, respectively, of the total number of diatoms at those sites and was generally found in relatively high numbers at all remote sites with no obvious human disturbance. *Gomphonema* dominated at all of the other eight sites, making up more than 50% of the total number of diatoms at Sites 4, 5, 6 and 8 (Table 4), all of which had moderate human disturbance scores.

The highest mean number of genera was obtained at Site 3 (20 ± 1.5) and the lowest at Site 4 (7.7 ± 1.5) (Table 5). Site 4 was the only site with a mean of fewer than ten diatom genera. The Shannon diversity index ranged from a high of 1.9 to a low of 0.9. Sites 2, 3, 10 and 11 showed relatively high levels of diatom diversity, while Sites 4 and 8 showed the lowest diversity of diatoms as well as the lowest evenness (Table 5). Taxa evenness ranged from 0.4 at Site 4 to 0.7 at Sites 3 and 9. There were no significant differences in the number of genera per site, the Shannon diversity index and the Pielou evenness index among the ten sites (Kruskal-Wallis ANOVA, $P > 0.05$). The number of genera per site and Shannon diversity was positively and significantly correlated with dissolved oxygen, while the number of genera was also significantly and negatively correlated with ammonium–nitrate concentration (Spearman correlation, $P < 0.05$).

The relative abundances of *Achnanthidium*, *Denticula*, *Pinnularia*, *Rhopalodia* and *Stauroneis* were negatively and significantly correlated with the disturbance score (Spearman Rank correlation, $P < 0.05$) (Table 6), suggesting that increases in human activities in the shallow marginal waters of the basin resulted in reduced abundance of these genera. The abundance of *Gomphonema* was significantly and positively correlated with the disturbance score (Spearman Rank correlation, $P < 0.05$) (Table 6), suggesting that *Gomphonema* was more tolerant of human impacts within the shallow marginal waters than other genera. The abundances of five genera (*Achnanthes*, *Cymbella*, *Denticula*, *Encyonema* and *Pinnularia*) were negatively and significantly correlated to total P, those of two genera (*Bacillaria* and *Mastogloia*) with nitrate–N (NO_3^-), those of two genera (*Diatoma* and *Navicula*) with ammonium–N (NH_4^+) and those of two genera

Table 2 Criteria for the human disturbance scores[a] within 500 m of the shore zone of Sanyati Basin

Activity	Site number									
	1	2	3	4	5	6	7	8	9	10
Residential area	0	0	0	0	0	0	0	3	1	1
Commercial aquaculture activities	0	0	0	3	0	3	0	2	0	0
Maintenance of boats and boating activities	0	0	0	2	3	1	3	2	3	2
Hotel/lodges/chalets	0	0	0	0	0	1	2	0	1	0
Road and vehicle density	0	0	0	3	2	2	3	3	3	2
Urban development	0	0	0	2	2	2	3	3	3	2
Industrial development	0	0	0	1	3	0	1	3	3	1
Active construction activities	0	0	0	3	3	0	0	3	3	2
Sewage effluent disposal	0	0	0	0	0	3	0	0	0	0
Effluent disposal from farming activities	0	0	0	3	0	2	0	0	0	0
Domestic human activities (washing and bathing)	0	0	0	0	0	0	0	3	0	0
Total disturbance score[b]	0	0	0	17	13	14	12	22	17	10
Human disturbance category[c]	N	N	N	M	M	M	M	M	M	L

[a] The impact of each activity or development at each site was assessed qualitatively on a scale of 0 (not occurring at the site) through 1 (low) and 2 (medium) to 3 (high)

[b] Overall total human disturbance score used for categorizing each site into one of four categories: 0, no evident disturbance; 1–11, little disturbance;12–22, moderate disturbance; 23–33,much disturbance

[c] The human disturbance category within which each site fell is represented by N = none or no disturbance, L = low, M = medium and H = high

Table 3 Mean (±SE) levels of selected physical and chemical variables of the water at the ten sites (n = 3 for variables at each site except where indicated otherwise)

Physical and chemical water variables	Site number 1	2	3	4	5	6	7	8	9	10
Temperature	25.5 ± 0.5	27.4 ± 0.9	26.0 ± 0.8	24.9 ± 0.2	24.4 ± 1.0	25.2 ± 1.7	26.2 ± 0.5	25.8 ± 0.8	25.3 ± 1.2	25.0 ± 0.9
Dissolved O_2 (mg l^{-1})	5.25 ± 0.35	5.75± 0.25	5.30 ± 0.30	4.00 ± 0.10	4.80 ± 0.50	4.85 ± 0.15	4.25 ± 0.35	4.30 (n = 1)	4.90 ± 0.50	4.45 ± 0.55
Conductivity (μS cm^{-1})	101.2 ± 1.4	99.2 ± 0.8	95.7 ± 1.3	99.2 ± 2.7	96.7 ± 0.6	95.4 ± 0.6	81.5 ± 17.0	97.1 ± 0.7	96.5 ± 0.6	95.1 ± 0.2
Total dissolved salts (mg l^{-1})	41.5 ± 0.5	40.5 ± 0.5	39.3 ± 0.3	40.3 ± 1.3	39.7 ± 0.3	39.0 ± 0.0	40.0 ± 0.0	40.0 ± 0.0	39.3 ± 0.3	39.0 ± 0.0
pH	7.7 ± 0.3	8.3 ± 0.1	8.6 ± 0.1	7.0 ± 0.6	6.7 ± 0.3	8.2 ± 0.4	7.1 ± 0.1	7.4 ± 0.1	7.0 ± 0.3	7.2 ± 0.1
Turbidity (NTU)	16.5 ± 1.5	4.4 ± 0.7	7.3 ± 1.3	15.6 ± 2.5	10.9 ± 3.4	19.4 ± 7.8	8.0 ± 2.1	2.1 ± 0.1	5.8 ± 1.5	5.6 ± 2.7
Ammonium–N (NH_4^+) (μg l^{-1})	62.7 (n = 1)	25.0 (n = 1)	31.7 ± 7.5 (n = 2)	48.5 ± 28.2 (n = 2)	18.8 ± 1.1 (n = 2)	30.8 ± 0.7 (n = 2)	31.7 ± 3.7 (n = 2)	21.6 ± 5.6 (n = 2)	20.7 ± 3.6 (n = 2)	12.2 ± 3.0 (n = 2)
Nitrate–N (NO_3^-) (μg l^{-1})	42.8 (n = 1)	27.6 (n = 1)	21.7 ± 11.0 (n = 2)	37.5 ± 25.3 (n = 2)	26.7 ± 3.5 (n = 2)	22.8 ± 14.2 (n = 2)	22.5 ± 13.9 (n = 2)	20.3 ± 7.7 (n = 2)	20.8 ± 10.7 (n = 2)	16.1 ± 8.0 (n = 2)
Phosphates (PO_4^{3-}) (μg l^{-1})	1.4 (n = 1)	1.4 (n = 1)	2.5 ± 0.4 (n = 2)	11.0 ± 5.2 (n = 2)	2.7 ± 2.1 (n = 2)	4.3 ± 2.2 (n = 2)	2.4 ± 1.4 (n = 2)	5.3 (n = 1)	7.8 ± 6.0 (n = 2)	2.9 ± 0.8 (n = 2)
Total phosphorous (μg l^{-1})	1.8 (n = 1)	1.4 (n = 1)	12.5 ± 9.6 (n = 2)	26.7 ± 10.4 (n = 2)	11.6 ± 8.5 (n = 2)	14.9 ± 3.6 (n = 2)	18.6 ± 0.9 (n = 2)	9.2 ± 3.9 (n = 2)	15.2 ± 1.4 (n = 2)	4.0 ± 3.9 (n = 2)
Sulphates SO_4^{2-} (mg l^{-1})	1.5 (n = 1)	1.2 (n = 1)	2.6 ± 1.5	4.1 ± 3.2	2.1 ± 1.3	2.3 ± 1.1	2.1 ± 1.3	2.0 ± 1.1	2.8 (n = 1)	1.8 ± 1.0

Table 4 Percentage relative abundances of periphytic diatoms associated with *Vallisneria aethiopica* in the shallow marginal waters of Sanyati Basin

Periphytic diatoms	Site number									
	1	2	3	4	5	6	7	8	9	10
Achnanthes	0.6	2.0	0.1	0.1	0.5	0.2		0.2	1.1	
Achnanthidium	63.1	20.5	41.1	0.4	16.1	7.4	19.8	9.7	23.7	27.5
Actinella			2.2							
Amphora	0.7	0.5	1.0	0.1		9.2	0.3	1.5	0.2	2.1
Aneumastis						0.1	0.3			
Aulacoseira		0.2	0.7	0.1	0.4	0.2	0.1		2.1	
Bacillaria			1.4		0.5	0.8	4.4		2.4	1.5
Cocconeis	0.4	2.9	11.4	20.3	3.6	0.8	0.3	0.6	1.8	0.5
Cyclotella	0.1				0.1		0.1		0.2	
Cymatopleura			0.1							
Cymbella	0.1	0.6	0.3		0.2	0.9	0.2	0.2		0.3
Denticula	0.3	2.5	0.9		0.3	1.6	0.3			0.8
Diatoma	0.1	0.5	0.2	0.3	0.5	0.3	0.5	3.1	3.2	2.1
Diatomella			3.6						0.2	
Didymosphenia			0.1							
Diploneis	0.1	0.2			0.1			0.2	0.1	0.3
Encyonema	2.3	2.0	1.2	0.1	0.8	1.1	0.4	0.8	1.4	1.8
Epithemia		0.2	0.4		0.2	0.1	0.1	0.3	0.2	
Eunotia		0.5			0.3		0.1	0.5	0.2	0.3
Fragilaria	1.9	4.3	2.0	2.1	3.0	3.3	3.4	1.4	2.1	2.5
Frustulia	1.0									
Gomphonema	16.0	45.5	10.3	69.0	56.1	60.1	47.2	72.2	32.9	35.9
Gyrosigma	0.3	0.2	0.1				0.1		0.1	0.1
Hantzschia									0.1	
Martyana			0.1							
Mastogloia	0.3	0.2	1.4		0.1		0.5	0.3	1.3	1.4
Melosira		0.2								
Navicula	3.9	4.6	3.3	1.3	4.3	4.5	4.5	3.7	11.1	4.7
Nitzschia	3.0	6.3	6.7	3.7	7.0	3.3	9.2	2.8	11.5	11.6
Opephora									0.1	
Pinnularia	0.7	1.1	0.5		0.5		0.4	0.9	0.4	0.4
Placoneis									0.1	
Pseudostaurosira			0.4	0.1			0.1			
Rhoicosphenia	0.1	0.2	0.6		0.7	1.7				0.3
Rhopalodia	1.2	0.8	2.9	0.1	0.3	0.3		0.2	0.3	0.5
Sellaphora										0.1
Stauroneis	2.5	3.2	1.9		1.4	0.3	1.9	1.1	1.1	2.2
Surirella		0.3	0.1			0.4		0.3	0.2	0.1
Synedra	1.2	1.1	4.7	2.4	3.3	3.8	6.0	0.3	2.0	3.0
Tabellaria	0.6		0.4							
Number of samples	2	2	3	3	3	3	3	2	3	3
Total no. of diatoms	726	653	1347	1005	1100	1166	1103	650	1062	1181
Number of taxa	22	25	30	14	23	21	23	20	27	23

(*Eunotia* and *Mastogloia*) with turbidity. Thus, the relative abundances of 13 diatom genera associated with *V. aethiopica* decreased with increasing disturbance score in the shallow waters of the Sanyati Basin.

Of the 16 DIBI metrics, 11 were significantly correlated with at least one of the 12 environmental variables (Table 7); 9 of the 16 metrics used in calculating the DIBI were significantly correlated with the DIBI (Table 7). Among the environmental variables the disturbance score was the only one that was significantly and inversely correlated with the DIBI (Table 7).

The DIBI scores ranged between 113.8 (Site 4) and 145.9 (Site1) (Table 8). There were significant differences in DIBI scores among the sites

Table 5 Mean number of genera, diversity and evenness (±SE) at ten sites along the shores of Sanyati Basin

Site	Number of genera	Shannon diversity (H')	Pielou evenness (J')
1	17.5 ± 2.5	1.4 ± 0.1	0.5 ± 0.1
2	19.0 ± 2.0	1.8 ± 0.2	0.6 ± 0.1
3	20.0 ± 1.5	1.9 ± 0.2	0.7 ± 0.0
4	7.7 ± 1.5	0.9 ± 0.2	0.4 ± 0.1
5	16.0 ± 1.5	1.5 ± 0.1	0.5 ± 0.0
6	14.7 ± 1.8	1.5 ± 0.3	0.6 ± 0.1
7	14.3 ± 3.3	1.6 ± 0.3	0.6 ± 0.1
8	14.0 ± 5.0	1.0 ± 0.6	0.4 ± 0.2
9	19.3 ± 1.2	1.9 ± 0.0	0.7 ± 0.0
10	17.7 ± 0.7	1.8 ± 0.1	0.6 ± 0.0

(ANOVA, $F_{9,\ 17} = 4.21$, $P = 0.005$). The DIBI scores at Sites 1 and 3 were significantly greater than those at Sites 2, 4, 5, 6, 7 and 8. Site 4 also had DIBI scores that were significantly lower than those at sites 7, 9 and 10. Thus, in general, remote sites with lower human activities had higher DIBI scores than those located where human activities were high. These data suggest that increases in human disturbances result in a decrease in the biological integrity of the diatom community associated with *V. aethiopica* in the shallow marginal water of Sanyati Basin.

Discussion

This study is the first to examine the responses of periphytic diatoms to human activities in a water body in Zimbabwe. Diatoms have been used successfully elsewhere to determine the ecological conditions of water bodies (Squires et al. 1979; Duncan and Blinn 1989; Bahls et al. 1992; Hardwick et al. 1992; Biggs and Hickey 1994; van Dam et al. 1994; Hill et al. 2000; Blinn and Bailey 2001; Köster and Hübener 2001). Most of the work on the use of diatoms has largely concentrated on epilithic diatoms in lotic systems. The present study has shown that periphytic diatoms on *V. aethiopica* may be used as tools to assess the impact of human activities on shallow inshore areas of a lentic system, Lake Kariba.

The most abundant genus at remote sites with no human disturbance was *Achnanthidium*, while at those sites with increased human activities *Gomphonema* dominated the diatom assemblage. The study showed that *Achnanthes*, *Cymbella*, *Denticula*, *Encyonema* and *Pinnularia* were sensitive to increased concentration of total P, *Bacillaria* and *Mastogloia* to an increase in nitrate–N, *Diatoma* and *Navicula* to an increase in ammonium–N and *Eunotia* and *Mastogloia* to turbidity. A number of other studies have also shown that diatom communities are affected by changes in physical and chemical variables, including changes in the concentrations of nutrients (Bahls et al. 1984; Charles 1985; Anderson et al. 1990).

The diatom assemblages from most of the sites located in remote areas and subjected to minimal human impact had relatively higher numbers of diatom genera and higher indices of diversity and community evenness than sites located in areas with relatively higher levels of human disturbance. The use of biotic indices is a water quality assessment approach that has been developed to avoid shortcomings associated with using the indicator species and community structure (richness, diversity, evenness) approaches (Hill et al. 2000). We found that although the number of genera, diversity and evenness tended to be higher at remote areas with minimal human disturbance, there were no significant differences among sites; in addition, the number of genera, diversity and evenness showed no significant correlations with the level of human disturbance. Unlike the indices based on community structure, the DIBI was more responsive to disturbance and showed a significant and inverse correlation with human disturbance.

In this study generic rather than species level resolution was used largely due to the limited information available on both the taxonomy of diatoms and diatoms in general in the Southern Africa region as well as the need to develop an easy-to-use, cost-effective diatom-based monitoring system for the lake that can be used by non-experts in algal taxonomy. The study revealed that human impact on the shallow water zones of Lake Kariba could potentially be evaluated using genus level taxonomic resolution of diatoms. Although there is some debate on the use of genus versus species level identification for assessing the quality of freshwater environments,

Table 6 Spearman correlation coefficients[a] for the relationship between percentage relative abundances of the periphytic diatoms, disturbance scores and selected physical and chemical characteristics of the water in the shallow marginal zones of Sanyati Basin

	Disturbance score	Temperature	Dissolved O_2	Conductivity	Total dissolved solids	pH	Turbidity	NH_4^+	NO_3^-	PO_4^{3-}	Total phosphorous	SO_4^{2-}
Achnanthes	0.01	0.26	0.21	**0.39**	0.30	0.02	–0.03	–0.02	0.45	0.31	**–0.49**	–0.44
Achnanthidium	**–0.60**	0.26	0.23	–0.02	0.14	0.14	–0.01	–0.04	–0.03	–0.14	–0.42	–0.16
Actinella	–0.26	0.13		–0.23	–0.19	0.25	–0.05	0.30	–0.21	–0.12	0.35	0.36
Amphora	–0.04	**0.45**	–0.32	–0.23	–0.10	0.29	–0.12	0.09	–0.12	–0.22	–0.07	0.04
Aneumastis	0.03	–0.22	–0.01	0.12	–0.04	–0.03	0.24					
Aulacoseira	0.05	0.10	0.31	–0.15	–0.31	0.21	–0.15	0.20	0.07	0.20	0.20	0.14
Bacillaria	–0.09	**–0.44**	0.37	–0.20	–0.28	–0.05	–0.24	0.07	**–0.66**	0.10	0.33	0.41
Cocconeis	0.15	–0.16	0.18	0.22	–0.03	0.03	0.09	–0.16	0.12	0.45	–0.07	–0.08
Cyclotella	–0.01	–0.07	0.13	0.19	0.15	–0.07	0.35	–0.16	0.12	–0.35	–0.21	–0.36
Cymatopleura	–0.26	–0.19	0.32	–0.30	–0.19	0.23	–0.09					
Cymbella	–0.13	0.38	0.03	0.02	–0.05	0.29	0.22	–0.10	0.05	0.29	**–0.52**	–0.33
Denticulata	**–0.46**	–0.07	**0.50**	0.00	–0.06	0.15	–0.13	0.04	0.22	0.00	**–0.64**	–0.25
Diatoma	0.18	–0.10	–0.09	–0.02	–0.08	–0.28	–0.33	**–0.61**	–0.36	0.10	–0.15	–0.07
Diatomella	–0.04	–0.33	0.32	–0.16	–0.06	–0.02	–0.24	–0.05	–0.26	0.26	0.12	0.08
Didymosphenia	–0.26	0.24	0.09	0.18	0.12	0.33	0.03	–0.05	0.21	0.21	–0.26	–0.15
Diploneis	–0.10	0.22	–0.07	0.04	0.06	–0.16	–0.28	–0.30	0.27	0.14	–0.46	–0.20
Encyonema	–0.33	0.18	0.14	0.01	–0.01	0.15	–0.17	–0.06	–0.21	0.08	**–0.47**	–0.05
Epithemia	0.10	0.05	0.32	–0.10	–0.11	0.08	–0.24	–0.28	0.02	–0.07	–0.05	–0.20
Eunotia	0.09	–0.12	0.22	–0.01	0.06	–0.13	**–0.53**	–0.31	–0.37	0.20	–0.05	–0.10
Fragilaria	–0.16	–0.26	0.38	0.21	0.15	0.02	–0.14	0.27	–0.42	–0.09	0.43	**0.60**
Frustulia	–0.37	–0.00	0.22	**0.40**	**0.45**	0.09	0.34	0.35	0.35	–0.23	–0.30	0.00
Gomphonema	**0.58**	–0.02	–0.38	–0.15	–0.16	–0.27	–0.08	0.01	0.15	0.05	0.33	–0.04
Gyrosigma	–0.33	0.15	0.34	0.36	0.24	0.19	–0.00	–0.43	0.00	–0.04	–0.20	–0.06
Hantzschia	0.22	0.28	–0.13	–0.03	–0.19	–0.15	–0.09	–0.26	0.16	–0.23	0.02	
Martyana	–0.26	–0.19	0.32	–0.30	–0.19	0.23	–0.09					
Mastogloia	–0.20	–0.20	0.22	–0.26	–0.21	–0.06	**–0.46**	–0.31	**–0.56**	0.06	0.23	0.27
Melosira	–0.26	0.33	0.26	0.20	0.12	0.18	–0.16	0.02	0.02	0.30	–0.35	–0.08
Navicula	–0.02	0.02	0.16	0.07	–0.06	–0.15	–0.25	**–0.59**	–0.15	0.07	–0.41	–0.21
Nitzschia	–0.08	–0.13	0.25	0.05	0.03	–0.05	–0.28	–0.39	–0.15	0.08	–0.23	–0.12
Opephora	0.22	–0.08	0.22	–0.14	–0.19	0.10	0.00					
Pinnularia	**–0.43**	**0.45**	0.25	0.01	0.06	0.22	–0.28	–0.33	0.13	0.04	**–0.50**	–0.35
Placoneis	0.22	–0.08	0.22	–0.14	–0.19	0.10	0.00		–0.26			
Pseudostaurosira	–0.06	–0.23	0.01	0.13	0.16	–0.02	0.17	–0.05	0.21	0.26	0.12	0.08
Rhoicosphenia	–0.31	0.31	0.14	–0.26	–0.27	**0.41**	0.19	0.02	–0.17	–0.02	–0.20	0.00
Rhopalodia	**–0.46**	–0.34	**0.62**	0.00	–0.04	0.33	–0.29	0.05	–0.20	–0.09	0.07	0.36
Sellaphora	–0.13	–0.23		–0.18	–0.19	0.03	–0.23	–0.40	–0.40	0.00	–0.12	0.08
Stauroneis	**–0.57**	0.15	0.25	–0.06	0.15	–0.02	–0.25	–0.24	–0.27	–0.16	–0.19	–0.01
Surirella	–0.03	–0.06	0.43	–0.08	–0.09	0.35	–0.33	–0.41	–0.15	0.43	–0.39	–0.16
Synedra	–0.08	**–0.50**	0.25	–0.03	–0.17	0.01	0.11	0.18	–0.44	0.11	0.39	0.36
Tabellaria	–0.37	0.02	0.31	–0.10	–0.06	**0.40**	–0.05	–0.05	0.21	0.21	–0.26	–0.15

[a] Significant correlations ($P < 0.05$) are presented in bold type

Table 7 Spearman correlation coefficients[a] for the relationship between the DIBI and its component metrics

Metric	Disturbance score	Temperature	Dissolved O_2	Conductivity	Total dissolved solids	pH	Turbidity	NH_4^+	NO_3^-	PO_4^{2-}	Total phosphorous	SO_4^{2-}	DIBI
Relative taxa richness	–0.36	0.11	**0.53**	–0.09	–0.12	0.30	–0.38	–0.38	–0.34	0.10	–0.23	–0.34	**0.68**
Dominant diatom metric	–0.37	0.08	0.32	0.00	–0.09	0.12	–0.24	–0.36	–0.27	0.10	–0.42	–0.27	**0.59**
Motile diatom	**0.50**	0.07	**–0.70**	–0.36	–0.32	–0.24	0.22	0.17	0.11	–0.19	0.40	0.11	–0.33
Acidophilic diatom	**0.57**	–0.29	**–0.54**	–0.13	–0.22	–0.28	0.35	0.22	–0.11	–0.05	**0.55**	–0.11	**–0.55**
Circumneutral diatom	**–0.73**	0.09	**0.60**	0.26	0.28	**0.41**	0.04	–0.02	–0.17	–0.05	–0.35	–0.17	**0.73**
Alkaliphilc	0.36	–0.08	**–0.59**	–0.27	–0.09	**–0.54**	–0.04	0.02	0.03	–0.22	0.23	0.03	–0.06
Nitrogen-autotrophic diatom (–1)	**–0.50**	0.04	0.29	0.15	0.16	0.22	0.13	–0.02	–0.18	–0.11	–0.30	–0.18	**0.82**
Nitrogen-autotrophic diatom (–2)	–0.10	0.06	–0.14	–0.06	0.18	–0.14	0.09	0.39	0.34	–0.36	0.12	0.34	–0.09
Oxygen requirement 1	**–0.52**	0.05	0.29	0.15	0.16	0.23	0.12	–0.02	–0.18	–0.11	–0.30	–0.18	**0.82**
Oxygen requirement 2	–0.07	0.04	–0.20	0.17	0.29	–0.18	0.28	0.37	0.30	–0.19	0.23	0.30	–0.25
Oxygen requirement 3	–0.15	0.16	–0.18	–0.22	0.03	–0.03	–0.09	0.16	–0.12	–0.45	0.07	–0.12	0.2
Oxygen requirement 4	0.09	**0.44**	–0.37	0.20	0.28	0.05	0.24	–0.07	**0.66**	–0.10	–0.33	**0.66**	–0.27
Oligo-mesotraphentic diatoms	**0.57**	–0.29	**–0.54**	–0.13	–0.22	–0.28	0.35	0.22	–0.11	–0.05	**0.55**	–0.114	**–0.55**
Mesotraphentic diatoms	**–0.72**	0.09	**0.55**	0.26	0.27	0.34	–0.03	–0.13	–0.26	–0.08	–0.32	–0.26	**0.77**
Meso-eutraphentic diatoms	**0.45**	–0.21	**–0.63**	–0.11	–0.03	**–0.50**	0.21	0.22	0.20	–0.09	0.45	0.20	**–0.48**
Eutraphentic diatoms	0.02	0.17	–0.23	–0.09	0.14	–0.12	0.03	0.23	0.28	–0.41	–0.14	0.28	–0.02
DIBI	**–0.64**	0.13	0.27	–0.01	0.11	0.14	0.06	–0.02	–0.16	–0.17	–0.32	–0.13	

[a] Significant correlations ($P < 0.05$) are in bold

Table 8 DIBI scores obtained from diatoms associated with *V. aethiopica* along the shallow marginal waters of Sanyati Basin

Site	*n*	Mean ± SE	DIBI score	
			Minimum	Maximum
1	2	142.9 ± 4.7	140.0	145.9
2	2	124.9 ± 4.7	118.9	130.9
3	3	140.9 ± 3.9	132.0	148.4
4	3	115.7 ± 3.9	113.8	117.2
5	3	126.0 ± 3.9	119.1	133.2
6	3	123.1 ± 3.9	117.1	127.3
7	3	129.0 ± 3.9	122.0	137.5
8	2	120.8 ± 4.7	113.7	127.9
9	3	130.6 ± 3.9	126.7	136.5
10	3	132.8 ± 3.9	125.5	138.6

a number of studies have found that while some information is lost, genus-based indices generally give acceptable indications of environmental quality (Kelly et al. 1995; Hill et al. 2001; Wunsan et al. 2002). Periphytic diatoms associated with *V. aethiopica* are therefore a potential tool that may be used to determine the ecological conditions of the shallow water margins in Sanyati Basin, and there is need for further exploration of their use for routine monitoring of the impact of anthropogenic activities, especially the development of a composite DIBI.

Conclusion

We report here the preliminary results of an ongoing study on the use of diatoms and macroinvertebrates as a tool for assessing ecological conditions within the shallow marginal waters of a large manmade reservoir, Lake Kariba. Although further work is necessary, this study shows that the diatom communities associated with *V. aethiopica* respond to differences and variations in human-induced effects in the shallow waters, thereby making them candidates for further development as freshwater biomonitoring tools in Zimbabwe.

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Appendix 5. Water physicochemical conditions at sampling Site 6 from August 2007 to August 2008.

Year	Month	Week	Temperature (°C)	pH	Conductivity (μS/cm)	Turbidity (NTU)	DO (mg/L)	DO (%sat)
2007	August	1	23.80	7.64	105.6	56.0	9.81	126.2
		2	25.47	7.25	105.0	13.0	9.62	123.7
		3	24.40	7.77	106.6	8.2	7.17	92.2
		4	24.56	7.55	105.8	25.7	8.87	114.0
	September	1	26.53	7.30	105.1	11.4	7.35	94.5
		2	25.03	7.36	112.9	15.9	5.84	75.1
		3	23.70	7.06	104.9	11.9	8.02	103.2
		4						
	October	1	27.50	7.71	103.3	20.5	8.91	114.5
		2	27.43	8.02	105.6	17.0	8.66	111.4
		3	27.80	8.22	104.2	21.7	7.97	102.5
		4	29.03	8.07	95.3	82.0	7.33	94.3
	November	1	28.20	7.95	99.8	53.9	7.63	98.2
		2	28.43	7.86	99.3	40.4	7.35	94.5
		3	32.95	8.52	98.3	43.7	7.20	92.6
		4	27.05	7.69	99.0	23.0	6.88	88.5
	December	1	28.38	7.93	108.0	40.3	5.32	68.4
		2	27.70	8.00	106.0	20.4	6.58	84.6
		3	29.72	8.09	97.6	21.6	7.04	90.5
		4						
2008	January	1	29.54	7.52	109.4	8.0	7.00	90.0
		2	27.52	7.55	100.3	8.2	7.39	95.1
		3	27.82	7.03	104.8	9.3	6.92	89.0
		4	31.27	9.68	103.9	15.7	7.94	102.1
	February	1	29.90	8.28	103.7	10.7	3.92	50.5
		2	28.97	7.58	100.9	22.1	5.98	76.9
		3	32.17	7.73	108.2	7.7	5.61	72.2
		4	31.27	7.65	101.5	5.2	6.73	86.6
	March	1	29.58	7.55	100.3	8.0	6.18	79.5
		2	29.63	7.62	101.1	7.3	7.09	91.1
		3	29.63	7.62	101.1	9.7	6.47	83.2
		4						
	April	1	28.00	7.78	98.5	26.8	6.34	81.6
		2	28.87	7.62	100.5	22.7	5.93	76.3
		3						
		4	29.00	7.70	124.1	10.5	6.65	85.6
	May	1	29.15	7.08	103.2		5.57	71.6
		2	28.63	6.94	130.4		5.52	70.9
		3	26.67	7.36	105.5	13.4	4.70	60.5
		4	24.83	7.25	110.0		4.89	62.9
	June	1	25.93	7.58	110.3	12.4	5.64	72.6
		2						
		3	25.00	7.39	126.5	5.3	7.15	92.0
		4	24.40	7.51	124.7	9.6	5.73	73.7
	July	1	25.20	7.77	143.0		6.24	80.2
		2	22.03	7.43	100.9		6.65	85.6
		3	24.47	8.01	102.9	7.7	5.57	71.6
		4	23.73	7.73		7.7	6.15	79.1
	August	1	24.50	7.61	104.5		6.49	83.5
		2						
		3	27.40	8.40	103.0	13.3	7.03	90.5
		4						

Appendix 5. Continued

Year	Month	Week	Total P (mg/L)	Phosphates (mg/L)	Total N (mg/L)	Ammonium (mg/L)	Nitrates (mg/L)	Dam Level (m)
2007	**August**	**1**	0.980	0.005	2.165	0.019	0.004	481.47
		2	0.663	0.005	2.361	0.017	0.004	481.34
		3	1.034	0.015	8.569	0.011	0.159	481.18
		4	0.892	0.008	4.365	0.016	0.055	481.06
	September	**1**	0.675	0.023	2.079	0.003	0.039	480.91
		2	0.237	0.024	4.347	0.005	0.100	480.79
		3	0.205	0.010	1.848	0.009	0.023	480.62
		4						480.47
	October	**1**	0.738	0.016	4.997	0.014	0.178	480.30
		2	0.441	0.002	5.084	0.103	0.115	480.12
		3	0.644	0.057	3.490	0.026	0.101	479.94
		4	0.775	0.161	3.484	0.057	0.079	479.75
	November	**1**	0.402	0.004	6.287	0.053	0.004	479.61
		2	0.271	0.012	5.490	0.018	0.004	479.50
		3	0.033	0.030	11.674	0.054	0.081	479.35
		4	1.903	0.007	3.952	0.013	0.579	479.19
	December	**1**	0.064	0.005	5.674	0.007	0.550	479.02
		2	0.699	0.018	7.780	0.053	0.827	478.97
		3	0.894	0.008	2.892	0.013	1.041	479.10
		4						479.50
2008	**January**	**1**	0.264	0.059	2.938	0.054	0.163	480.38
		2	0.063	0.023	4.245	0.047	0.041	480.80
		3	0.147	0.025	4.976	0.248	0.219	481.08
		4	0.052	0.023	3.909	0.066	0.042	481.56
	February	**1**	0.026	0.027	4.561	0.102	0.074	482.37
		2	0.032	0.040	4.334	0.265	0.035	482.57
		3	0.126	0.037	2.118	0.422	0.023	482.65
		4	0.080	0.006	5.049	0.004	0.107	482.74
	March	**1**	0.073	0.008	6.643	0.010	0.185	482.96
		2	0.077	0.011	7.114	0.024	0.095	483.21
		3	0.347	0.033	2.096	0.038	0.079	483.52
		4						483.75
	April	**1**	0.428	0.020	1.476	0.029	0.023	483.92
		2	0.129	0.009	1.401	0.038	0.018	484.04
		3						484.23
		4						484.37
	May	**1**						484.53
		2						484.70
		3						484.82
		4						484.91
	June	**1**						485.00
		2						485.04
		3						485.04
		4						485.03
	July	**1**						485.00
		2						484.94
		3						484.84
		4						484.71
	August	**1**						484.57
		2						484.43
		3						484.28
		4						484.12

Appendix 6. Eigen vectors (Coefficients in the linear combinations of variables making up PC's) of physicochemical parameters.

Variable	PC1	PC2	PC3	PC4	PC5
Temperature	-0.233	0.427	0.184	0.344	0.090
PH	-0.259	0.220	0.031	-0.083	0.568
Conductivity	0.325	-0.107	0.028	0.271	-0.093
Turbidity	-0.353	-0.020	-0.451	-0.157	-0.031
DO	-0.241	-0.382	-0.247	0.261	0.291
Total P	-0.282	-0.436	0.002	-0.060	-0.316
PO_4^{2-}	-0.227	0.222	-0.544	0.006	-0.344
Total N	-0.395	0.047	0.246	0.296	0.184
NH_4^-	0.006	0.397	-0.046	0.489	-0.412
NO_3^{2-}	-0.268	-0.095	0.576	-0.205	-0.365
Dam level	0.472	0.105	-0.098	-0.064	0.136

Appendix 7. Principal component scores showing contribution to the five PCs by physicochemical conditions on each sampled date during the study period.

Sample	SCORE1	SCORE2	SCORE3	SCORE4	SCORE5
Aug-07	***-1.210***	***-3.390***	***-2.010***	0.421	0.420
Aug-07	0.026	***-2.890***	***-0.613***	1.250	0.331
Aug-07	***-0.983***	***-2.450***	0.734	1.040	0.075
Aug-07	***-0.770***	***-2.930***	***-0.613***	0.919	0.259
SEP	0.111	***-1.980***	***-0.322***	0.821	***-0.387***
SEP	0.377	***-0.398***	0.148	***-0.457***	***-0.518***
SEP	0.592	***-1.250***	***-0.429***	***-0.716***	***-0.198***
OCT	***-1.580***	***-1.640***	0.015	0.574	0.374
OCT	***-1.250***	***-0.207***	0.301	0.545	0.689
OCT	***-1.910***	***-0.004***	***-0.961***	***-0.348***	0.182
OCT	***-4.570***	1.500	***-4.830***	***-1.210***	***-1.830***
NOV	***-2.300***	0.172	***-0.696***	***-0.290***	0.869
NOV	***-1.820***	0.271	***-0.458***	***-0.429***	0.864
NOV	***-3.690***	2.170	0.200	0.748	1.830
NOV	***-2.840***	***-2.170***	1.560	***-1.450***	***-1.830***
DEC	***-1.710***	0.528	1.630	***-0.944***	***-0.214***
DEC	***-2.660***	***-0.951***	2.500	0.290	***-1.030***
DEC	***-3.080***	***-0.616***	2.910	***-1.530***	***-1.220***
JAN	***-0.537***	0.708	***-0.259***	0.353	***-0.811***
JAN	***-0.303***	0.567	0.048	***-0.202***	0.322
JAN	***-0.116***	1.250	0.470	1.310	***-1.870***
JAN	***-1.670***	2.050	0.057	0.276	3.120
FEB	0.077	2.690	0.827	***-0.219***	0.200
FEB	***-0.187***	2.460	***-0.550***	1.190	***-1.200***
FEB	0.405	3.740	***-0.054***	2.720	***-2.040***
FEB	***-0.106***	1.080	1.100	***-0.023***	0.935
MAR	***-0.088***	0.795	1.270	***-0.034***	0.594

Appendix 7. Continued

Sample	SCORE1	SCORE2	SCORE3	SCORE4	SCORE5
MAR	***-0.037***	0.011	0.810	1.310	1.040
MAR	0.453	***-0.136***	***-0.120***	0.981	0.017
APR	0.285	***-0.404***	***-0.626***	0.202	0.325
APR	0.882	0.140	***-0.157***	0.381	0.407
APR	1.900	0.140	0.030	0.627	0.347
MAY	1.630	0.944	0.120	***-0.743***	***-0.493***
MAY	2.870	***-0.124***	0.137	0.815	***-0.891***
MAY	2.000	0.861	0.080	***-1.210***	***-0.446***
MAY	2.460	0.132	***-0.091***	***-0.935***	***-0.613***
JUN	2.040	0.359	***-0.121***	***-0.822***	0.002
JUN	2.820	***-1.250***	***-0.283***	0.895	0.018
JUN	2.780	***-0.049***	***-0.138***	***-0.651***	***-0.253***
JUL	3.300	***-0.992***	***-0.116***	1.170	0.119
JUL	2.040	***-0.345***	***-0.540***	***-1.660***	0.004
JUL	1.800	0.591	***-0.073***	***-1.490***	0.537
JUL	1.930	0.135	***-0.258***	***-1.390***	0.293
Aug-08	1.800	0.082	***-0.353***	***-1.190***	0.235
Aug-08	0.835	0.798	***-0.272***	***-0.890***	1.440