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The Ecology of Sua pan and its Flamingo Populations

Graham McCulloch

A THESIS SUBMITTED TO THE UNIVERSITY OF DUBLIN FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

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This thesis is dedicated to Allistair Torr, a good friend and an enormous inspiration, who died tragically in a plane crash while researching elephants in the Okavango Delta.

Declaration

I hereby declare that this thesis, submitted to the University of Dublin for the degree of Doctor of Philosophy, is entirely my own work, unless otherwise stated. I also certify that this thesis has not been submitted previously to this or to any other university.

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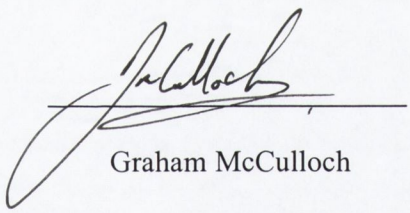

Graham McCulloch

July 2003

Summary

Sua pan is part of the Makgadikgadi saltpan complex, which is derived from an ancient palaeo-lake that once covered much of present-day northern Botswana. Today it is the 'sump' of an endorheic drainage system, into which various inland rivers flow intermittently to form a shallow saline wetland. Sua pan is also well known as one of the most important breeding sites in southern Africa for Lesser (*Phoeniconaias* minor) and Greater Flamingos (*Phoenicopterus ruber roseus*) that migrate from all over southern Africa to breed. Because water in the pan is ephemeral numbers arriving and subsequent breeding success depends on the amount of flooding each year. Before the work described in this thesis, no detailed studies had been carried out on the limnology of this important wetland ecosystem. The aim of this research was to identify the main physical and chemical factors that control ecosystem functioning during two wet seasons and quantify the species, standing crop biomass and production of the main biological components in the food web. Greater and Lesser Flamingo population and breeding estimates were monitored and discussed in terms of food availability and 'good' breeding conditions. The amount of water input onto Sua pan was quantified by collating daily rainfall data from the river catchments and pan area, river discharge data from the inflowing rivers and potential evapotranspiration data. The area of flooding was determined from satellite images of the pan and flood periods were calculated from combined water input and daily evaporation rates. The largest estimated input of water varied between the basins on Sua pan and came mainly from direct rainfall, with Nata River discharge contributed almost 50% of the input onto the north basin. Groundwater input and output may also have had a large influence on the pans hydrological regime given the shorter predicted flood periods compared with observed flood periods, but its contribution is unknown. pH and conductivity were measured weekly in each basin over two wet seasons and ionic composition and nutrient concentrations were analysed from monthly samples of each basin and three inflowing rivers. Pan salinity varied both spatially and temporally, ranging between 320 to 111000 $\mu S\ cm^{-1}$, and resulted mainly from surface evaporites and saline groundwater brine. Pan salinity comprised the dominant ions Na^+ and Cl^-, although HCO_3^- was also important, contributing to high pH values of between 8.5 and 10. Total phosphorus and total nitrogen in the pan generally

increased as the basins dried up, with maximum values of, respectively 2 and 6.3 mg l^{-1}. Samples of chlorophyll a, phytoplankton and epipelic periphyton were collected weekly from each basin during two wet seasons. Standing crop biomass was estimated and production was calculated using daily P:B ratios form the literature. The flora of the pan was dominated by the filamentous cyanobacteria *Nodularia*, while *Oscillatoria* and *Spirulina* were less abundant. *Navicula* and *Nitzschia* were the dominant diatoms and were most abundant in very shallow water and on exposed mud surfaces. Phytoplankton biomass and productivity on Sua pan varied considerably both spatially and temporally, but maximum estimates were similar to those in some of the most productive lakes in Africa. This was attributed to a combination of physical and chemical factors that influenced favourable light, temperature and high nutrient concentrations. Weekly samples of zooplankton and benthic crustaceans were also taken in each basin using two sampling techniques, and the dominant species counted, measured and weighed to calculate biomass and production. Crustacean species richness was generally low, although varied spatially and temporally and decreased with increasing salinity. Five species dominated abundance, *Branchinella spinosa*, *Br. ornata*, *Moina belli*, *Lovenula africana* and *Limnocythere tudoranceai*. Secondary production of the most common species was similar to estimates from the most productive lakes in Africa. Flamingo numbers and breeding success were monitored from the air on a monthly basis over two breeding seasons. Greater and Lesser Flamingo populations reached maxima of, respectively, 57800 and 149400, exceeding totals estimated for both populations in southern African. Estimated from aerial monitoring of the breeding colonies during the 1999-2000 breeding season, 47600 Greater Flamingo raised 18500 chicks and 128000 Lesser Flamingo raised 30600 chicks. Greater and Lesser Flamingo diet was determined from faecal and opportunistic crop sampling and mostly comprised dominant crustaceans and algae and diatoms. During the breeding season, an abundant food supply close to the breeding site was recognised as a very important factor controlling breeding success and the survival of flamingo chicks to recruitment. Using PTT satellite tracking devices, individuals of each species were tracked during their migrations from the pans back to their non-breeding sites, which were scattered throughout southern Africa. Nocturnal highly dispersed movements among numerous large and small wetlands during the non-breeding season highlight their nomadic behaviour and a dependence on a network of wetlands.

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Chapter 1

General introduction

1.1 Temporary saline lakes: geology, morphology and hydrology

Inland saline lakes are a common feature on every continent, and in dry climates are sometimes the only sources of surface water. The term atthalassohaline is used to refer to saline waters that have no direct marine connection (Williams, 1998). For saline lakes to occur, water loss by evaporation exceeds the volume of water entering the lake from surface inflow and direct precipitation, so that solutes in the water accumulate and salinity increases (Hutchinson, 1957; Eugster & Hardie, 1978; Hammer, 1986; Williams, 1998). Certain geological and climatic conditions are necessary for this to happen. Firstly, there must be a suitable geomorphologic depression representing the terminus of a hydrologically closed drainage basin, i.e. a basin with no surface outflow (Hutchinson, 1957; Reeves, 1968). De Martonne & Aufrere (1928) were the first to describe such regions as endorheic, as opposed to exoreic regions that drain into the sea. These drainage basins have been predominantly categorised as tectonic, volcanic or glacial in origin, while wind deflation plays a role in the origin of some of the smaller shallow lake basins (Hutchinson, 1957; Hammer, 1986; Shaw & Thomas 1989; Allanson *et al.*, 1990). The amount and duration of standing water present in an endorheic basin is dependant upon variable combinations in rainfall, temperature and evaporation, over space and time (Langbein, 1961; Cole, 1968; Comin & Williams, 1994). Climate is, therefore, of extreme importance to the existence of saline lakes.

Temporary or ephemeral saline lakes occur in endorheic basins when water income or water loss, or both, is seasonal or intermittent and the lake experiences cyclic wet and dry phases (Hartland-Rowe, 1972; Williams, D.D., 1987; Williams, 1998). Decksbach (in Hartland-Rowe, 1972) refers to these temporary lakes as seasonally astatic waters. Aridity (irrespective of air temperature) is one of the main conditions necessary for the existence of intermittent lakes. UNESCO (1979) used an index based on the ratio of the mean annual precipitation and the annual potential evapotranspiration (PET) to derive four degrees of aridity: hyper-arid, arid, semi-arid, and sub-humid zones. Most temporary lakes are found in arid and semi-arid zones around the world (Hutchinson *et al.*, 1932; Hartland-Rowe, 1972; Allan *et al.*, 1995; Williams, 1998). While annual rainfall is a significant factor in the occurrence of temporary saline lakes in arid regions, the intensity of precipitation and river inflow has a profound effect on the duration of the wet phase. This results in unpredictable seasonal changes in the water

regime and a considerable change in the physical and chemical properties of the waters with each inundation period (Hartland-Rowe, 1972; Langbein, 1961; Seaman & Kok, 1987; Meintjes *et al.*, 1994; Allan *et al.*, 1995). Size and depth of the endorheic basin, assuming they are correlated (Neumann, 1959), also play a major role in the temporal dynamics of saline lakes. Temporary lake water levels and wet phase duration are highly variable, less predictable, and very sensitive to both short and long-term climatic events, owing, predominantly, to their shallow nature (Hartland-Rowe, 1972; Comin & Williams, 1994; Allan *et al.*, 1995; Williams, 1998). These temporal patterns of flood size duration play a major role in determining other physico-chemical characteristics, as well as the biota of these ecosystems (Williams D.D., 1987; Williams, 1985; 1990; Comin & Williams, 1994).

1.2 Saline lake water chemistry

1.2.1 Salinity

The most immediate effect of a change in the amount of standing water in a lake is the corresponding change in its salinity. All waters contain some dissolved salts or ions and the range and concentration of these ions determines salinity (Hutchinson, 1957; Williams & Sherwood, 1994). All sources of water input into a closed basin contain different concentrations of salts and, over the long term, these inputs control lake brine evolution (Talling & Talling, 1965; Kilham, 1971; Hardie & Eugster, 1978). Sources of salinity include cyclic salts (solutes in precipitation), geological deposits, hydrothermal springs, relictual sea water and salts derived from the weathering of the surrounding soils and rocks (Gorham, 1961; Bayly & Williams, 1973; Eugster & Hardie, 1978; Williams, 1998). The predominant loss of water from a closed system is through evaporation, which involves water alone, and this results in a constant concentration of salts through a process of evaporative concentration (Gibbs, 1970; Hardie & Eugster, 1970; Kilham, 1971). One would, therefore, expect a constant increase in salinity to saturation (e.g. Rawson & Moore, 1944). Some loss to groundwater and from the dry lake surfaces through wind action also occurs (Hutchinson, 1937; Langbein, 1961; Shaw & Thomas, 1989). Many authors have tried to place a boundary on the distinction between fresh and saline lakes (Hammer, 1986). A boundary of 3 g l^{-1}, set by Williams (1964), has become widely accepted. Hammer (1986) divided saline waters into

hypo-saline (~3-20 g l^{-1} or 3-20 $^{0}/_{00}$), meso-saline (~20-50 g l^{-1}), and hyper-saline (>50g l^{-1}). Salinity changes, and the variation in the ionic composition, among temporary saline lakes depend on the short-term instability and long-term unpredictability of environmental factors, mainly climatic, which result in wide geographical and temporal salinity variations (Hartland-Rowe, 1972; Seaman & Kok, 1987; Meintjes *et al.*, 1994).

1.2.2 Ionic composition

Saline lake brines are dominated by eight major solutes (Williams, 1998). Predominant cations are Na^{+}, K^{+}, Ca^{2+} and Mg^{2+}, and the major anions are Cl^{-}, SO_4^{2-}, HCO_3^{-} and CO_3^{-}. The relative proportions of these major ions may vary considerably among lakes and, as a result, saline lakes are characterised by their dominant ion combinations (Eugster & Hardie, 1978; Williams, 1998). Certain combinations show regional distributions, as in Australia (Williams & Buckney, 1976*a*, *b*), East Africa (Beadle, 1932; Talling & Talling, 1965; Kilham, 1990) and southern Africa (Day, 1993). This variation among lakes is coupled with the fact that spatial variability in salinity within temporary lakes is associated with changes in proportional ionic composition (Hartland-Rowe, 1972; Eugster & Hardie, 1978; Shaw & Thomas, 1989; Meintjes *et al.*, 1994).

1.2.3 Variability in salinity

Dahl (1956) used the term 'poikilohaline' to refer to water of variable salinity in marine environments. Later, Bayly (1967) used the saline lake equivalent 'poikilosaline' to describe lakes with variable salinities and highlighted its importance in controlling biological composition. Rawson and later Hammer (in Hammer, 1986) confirmed that seasonal variability increased as lake salinity increased. Williams (1964) stated that the biology of lake waters with higher salinities must withstand greater seasonal chemical variability than species in any other aquatic environment. This is generally true for most saline lakes (e.g. Weir, 1969; Horne & Viner, 1971; Hartland-Rowe, 1972; Meintjes *et al.*, 1994). Species that occur in temporary saline lakes must also withstand extreme temperature and cyclical droughts of varying duration (Rzoska, 1958; Weir, 1969; Hartland-Rowe, 1972; Williams D.D., 1987). Talling & Talling (1965), Cholnoky (1966), Ziemann (1968), Kilham (1971), Beadle (1974), Hecky & Kilham (1973), LaBarbera and Kilham (1974) and Williams (1978), have all recognised the importance of salinity as a primary controlling factor in the distribution and abundance of organisms in saline lakes. While it may be possible to categorize saline lakes

according to their flora and/or fauna on a local or regional scale, it is inappropriate to do so for saline lakes in general, owing to the large variation in species-specific tolerances to salinity. In addition, other lake-specific factors such as temperature, oxygen and nutrient levels can be highly variable among lakes of similar salinities and also influence biological composition (Hutchinson *et al.*, 1932; Hartland-Rowe, 1972; and Meintjes *et al.*, 1994). Even so, species richness and composition can be correlated with salinity over its entire range (Hecky & Kilham, 1973; LaBarbara & Kilham, 1974; Hammer, 1986; Williams *et al.*, 1990).

1.3 Other physico-chemical factors controlling lake biology

1.3.1 Oxygen

Variable oxygen concentrations occur on a diurnal and seasonal basis depending upon temperature, thermal stratification, wind action, algal photosynthesis and organic decomposition (Jenkin, 1936; Rawson & Moore, 1944; Hammer & Haynes, 1978; Ashton & Schoeman, 1983). Salinity has, however, a direct influence on the concentration of oxygen present in saline waters. The solubility of oxygen in water decreases significantly as salinity increases, and saturation occurs at lower concentrations, regardless of temperature (Sherwood *et al.*, 1992; Williams, 1998). During warm water conditions, highly saline lakes can have oxygen saturation concentrations that are limiting to some forms of biotic growth.

1.3.2 pH

pH is a measure of the hydrogen ion concentration, which, in turn, is controlled by the carbon dioxide equilibrium, $CO_2 - H_2CO_3 - HCO_3^- + H^+ - CO_3^{2-} + 2H^+$ (Stumm & Morgan, 1970). Changes result from the alternating input and removal of CO_2, which alters the relative concentrations of carbonic acid (H_2CO_3) and H^+ ions, but concentrations usually lie between pH 6.0 and 9.0 (Bayly & Williams, 1973). In many natural lakes, pH increases with salinity and most saline lakes have pH values >7, especially those with high Na and HCO_3^-/CO_3^{2-} proportions in their total ion concentration (Hutchinson, 1957; Talling & Talling, 1965; Bayly & Williams, 1973; Ashton & Schoeman, 1983; Williams, 1998). At very high salinities, pH can, however, decrease but few organisms are able to tolerate these extreme conditions. Mostly though, species tolerate a wide range of pH and, in terms of ecological significance, it

is an important indicator of other factors that may be more significant, such as CO_2 and dissolved organic nutrients.

1.3.3 Nutrients

Concentrations of phosphorus, nitrates, nitrites and ammonium salts are wide ranging among saline lakes (Hammer, 1986; Talling & Lemoalle, 1998). Phosphorus is transported either as a salt absorbed to soil particles, a form that is not immediately available for plant uptake, or as dissolved phosphorus. Catchments in semi-arid and arid regions facilitate the transportation of large amounts of particulate phosphorus into lakes, owing to sparse vegetation cover and a high degree of soil erosion. As a result, highly turbid saline lakes contain a large supply of phosphorus (Talling & Talling, 1965; MacLachlan, 1971; Howard-Williams, 1972; Gaudet & Muthuri, 1981; Ashton & Schoeman, 1983). Nitrogen takes on various forms, but nitrate and ammonium are the most important for the biota of saline lakes. Available nitrogen tends to occur in low concentrations in arid and semi-arid temporary waters (Talling & Talling, 1965). While concentrations vary, owing to varying combinations of nitrification, denitrification and nitrogen-fixing (e.g. Horne & Galat, 1985), it is commonly the limiting nutrient in warm saline lakes, where phosphorus is relatively abundant (Bayly & Williams, 1973; Horne & Goldman, 1994, Talling & Lemoalle, 1998). Internal loading of nutrients from the lake sediment is an important factor in saline lakes and lake morphology plays an important role in the extent of nutrient regeneration from the sediment (e.g. Moss & Moss, 1969; Marsden, 1989). Large shallow lakes, for example, facilitate nutrient recycling because a large proportion of the lake water is in contact with the sediment. Another important source of nutrient loading comes from the activities of birds and animals that feed and breed in these lakes. Large amounts of nutrients locked up in the biota of saline lakes can be recycled by the feeding activities of birds and made available again through their droppings (e.g. Marion *et al.*, 1994; Scherer *et al.*, 1995). Flamingo population numbers, for example, can reach millions of individuals (Berry, 1972; Brown, 1975; Parker, 1975) and may have a significant impact on the nutrient cycle of a shallow saline lake (Vareschi, 1978). In addition, their foraging activities stir-up muddy lakebeds and subsequently release of nutrients from the sediment (Glassom & Branch, 1997; Comin *et al.*, 1997).

1.3.4 Turbidity

The turbidity of a lake comprises small particles of suspended organic and inorganic matter in the water column, which affect the physical, chemical and biological properties of lake ecosystems (Noble & Hemens, 1978; Kirk, 1983; Hart, 1986; 1987). These particles are often mainly inorganic clay and mineral particles derived from lake sediments and inflowing rivers, and are recognised as an important contributor of nutrients (Murphy, 1962; Brylinsky, 1980). High phytoplankton concentrations can also reduce light incidence considerably (Jenkin, 1936; Walker, 1973; Ashton & Schoeman, 1983). Turbidity is particularly common in very shallow, often ephemeral lakes in arid and semi-arid regions, where temporary inflowing rivers contain characteristically high sediment loads and wind drives continual mixing and re-suspension of sediment (e.g. Hutchinson *et al.*, 1932; Hartland-Rowe, 1972; Talling *et al.*, 1973; Melack & Kilham, 1974; Livingstone & Melack, 1984). In these highly turbid waters light often penetrates no more than a few centimetres. While they can enhance the nutrient loading of a lake, large amounts of suspended particles also reduce temperature and incident light, and in turn the productivity potential of shallow saline lakes (Hammer, 1981; Kirk, 1983; Hart, 1988; Harding, 1997; Wetzel, 2001). Turbidity and light transparency decrease with increased salinity (Hammer, 1986). Wind induced turbulence increases turbidity in shallow lakes, ensuring frequent mixing of sediment in the water column. Thermal stratification rarely occurs in shallow lakes and they are said to be polymictic (Hammer & Haynes, 1978; Hammer, 1981; Vareschi, 1982). Hammer and Haynes (1978) found that lakes less than 4m mean depth did not generally stratify. Stratification may occur when the epilimnion warms up under calm conditions but breaks down as soon as wind causes mixing. Shallow lakes also have low heat storage potential, and extremely wide daily and seasonal ranges in temperature parallel air temperatures (Hartland-Rowe, 1972; Marchant & Williams, 1977).

1.4 Primary producers in saline lakes

The flora in lakes consists of three main groups, macrophytes (macroflora), phytoplankton, and periphyton (Horne & Goldman, 1994; Wetzel, 2001).

1.4.1 Macrophytes

Shallow saline lake macrophytes consist of higher aquatic plants such as reeds, sedges and grasses (Howard-Williams, 1979; Taylor, 1983; Iltis & Lemoalle, 1983; Hammer, 1986). Their contribution to the total floral biomass and primary production of these ecosystems varies depending on the amount of incident light, which is controlled by morphology (depth) and turbidity (Hammer, 1986; Talling, 1992; Wetzel, 2001). Indeed, water depth and turbidity have been identified as the main factors controlling the reduction of macrophytes in shallow lakes in southern Africa (Howard-Williams, 1979; Taylor, 1983; Allanson & Howard-Williams, 1984). Iltis & Lemoalle (1983) identified salinity changes, owing to decreasing water levels, as an important factor controlling macrophyte distribution. They appear, generally, to exist only at low salinities and submerged macrophytes are typically absent in saline lakes above 20 g l^{-1} (Hammer, 1986; Seaman *et al.*, 1991). Macrophytes are also unable to tolerate the highly dynamic lake level fluctuations characteristic of many shallow saline lakes (Allanson *et al.*, 1990; Talling & Lemoalle, 1998).

1.4.2 Periphyton

Periphyton algae grow on the submerged surfaces of stone (epilithic), higher plants (epiphytic) or sediment (epipelic) where light penetrates the overlying water column, predominantly, in the shallow littoral zone (Horne & Goldman, 1994; Wetzel, 2001). Light penetration to the lake substratum occurs over much of the area of shallow lakes and periphyton, therefore, make up a large proportion of total floral biomass and production in such conditions (Taylor, 1983; Hammer, 1986). The primary factors such as depth and turbidity that control macrophyte distribution also control these benthic algae by determining the amount of lake bottom lying within the euphotic zone (Dumont, 1992; Talling & Lemoalle, 1998; Bootsma & Hecky, 2001). Nutrient levels, grazing, and the availability and nature of the substratum are also important. Owing to the highly dynamic lake level changes in shallow lakes, the periphyton community tends to comprise species of diatoms and cyanobacteria that can tolerate large variations in salinity and varying periods of desiccation (Livingstone & Melack, 1984; Bauld, 1986; Dumont, 1992). Rich concentrations of cyanobacteria and pennate diatoms have been observed in the periphyton of shallow saline lakes in East Africa (Hecky & Kilham, 1973; Iltis, 1968; Melack, 1988) and southern Africa (Cholnoky, 1966; Moss & Moss, 1969; Howard-Williams & Allanson, 1981) although, generally, few studies have been carried out on the periphytic flora of African lakes (Talling & Lemoalle, 1998; Bootsma & Hecky, 2001).

1.4.3 Phytoplankton

Phytoplankton are primary producers suspended in the water column and are made up of a wide variety of algae, including green algae, cyanobacteria and diatoms (reviewed in Horne & Goldman, 1994; Talling & Lemoalle, 1998; Wetzel, 2001). An ability to move vertically, especially, among species of filamentous cyanobacteria, enables some phytoplankton to alter their position in the water column in response to changing light, nutrient and predatory conditions, according to daily cycles and climatic variation. This is, particularly, advantageous in shallow turbid lakes and favours filamentous cyanobacteria blooms close to the surface (Dumont, 1992). Vertical positioning, however, is also influenced by alternating wind induced turbulence and calm stratifying conditions that occur in many shallow saline lakes (Hammer, 1986; Dumont, 1992). In very shallow lakes the distinction between periphyton and phytoplankton is often difficult owing to the frequent wind induced mixing of the periphyton into the water column (Ganf, 1974*b*; Talling, 1992) and species composition is, therefore, very similar. Variation in horizontal distribution also occurs in phytoplankton communities owing to varying physical, chemical and biological conditions (Horne & Goldman, 1994). Sheltered parts of the lakes, for example, may experience calm settling conditions and corresponding clearer waters may encourage the proliferation of the periphyton communities, while dense concentrations of phytoplankton can be wind-driven to one side of a lake (Dumont, 1992).

1.5 Crustaceans of intermittent saline lakes in Africa

Planktonic crustaceans dominate faunal compositions among intermittent saline lakes in Africa (Hutchinson *et al.*, 1932; Williams, 1987; Day, 1990; Seaman *et al.*, 1991; Green, 1993). Since they dry out seasonally or episodically, organisms that can tolerate the harsh physical and chemical conditions inhabit temporary saline lakes associated with highly variable and unpredictable flood regimes (Hutchinson, 1967; Bishop, 1967; Brown & Carpelan, 1971; Belk & Cole, 1975; Hildrew, 1985; Kok, 1987; Hammer & Appleton, 1991). Resistant stages in their lifecycles enable them to survive extreme temperatures and prolonged desiccation, and an opportunistic lifecycle allows these animals to respond immediately to flooding, grow rapidly to reach maturity and reproduce in order to exploit short flood periods. Most species from the euphyllopoda (members of the orders anostraca, notostraca and

conchostraca) are confined to temporary waters, having requirements that can only be satisfied by the alternating wet and dry phases of these ecosystems (Broch, 1965; Bishop, 1967; Brown & Carpelan, 1971; Belk & Cole, 1975; Hildrew, 1985). As a result, they are typically absent, or uncommon, in permanent waters. Salt tolerant species of copepoda, anamopoda and ostracoda also occur in these ephemeral habitats, with stages of their life cycle also capable of resisting prolonged periods high salinity and desiccation (e.g. Hutchinson *et al.*, 1932; LaBarbara & Kilham, 1974; Williams, 1985; Martens, 1988; 1996; Day, 1990; Seaman *et al.*, 1991). In the early stages of flooding, crustacean species common to freshwater habitats can also inhabit these systems but die out as salinities increase (e.g. Seaman & Kok, 1987, Frey, 1993). While species richness is generally low, abundance can be very high (Hutchinson *et al.*, 1932; Hartland-Rowe, 1972; Seaman *et al.*, 1990; Allanson *et al.*, 1991). Crustaceans, therefore, provide a plentiful source of food for secondary consumers and one of the most efficient feeders of crustaceans in shallow saline lakes is the filter feeding Greater flamingo.

1.6 Flamingos in Africa

1.6.1 Distribution and abundance

Of the five species of flamingo that occur worldwide two, the Greater flamingo (*Phoenicopterus ruber roseus*, Linnaeus, 1758) and the Lesser flamingo (*Phoenicopterus minor*, Geoffroy Saint-Hilaire, 1798), occur in Africa. Both species occupy similar habitats and frequently coexist, often in large flocks numbering tens of thousands of birds (Allen, 1956; Berry, 1972; Brown, 1973; Brown, 1975; Hancock, 1990). The Greater flamingo is the larger, and the most widely distributed of the two species, occurring throughout Africa. Kahl (1975) estimated the total African population to be 165,000. More recent estimates, however, put the African population at approximately 85,000 (del Hoyo *et al.*, 1992; Simmons, 1996; 2000). Differences in population estimates highlights the difficulties of censusing a bird that is constantly moving between remote wetlands and occurs in such large numbers. The population of southern Africa has been estimated at between 47,000 (Simmons, 1996) and 55,000 (Dodman & Taylor, 1995, Harrison *et al.*, 1997).

Lesser flamingos are the most abundant flamingo species in the world and are almost entirely confined to Africa (Brown *et al.*, 1982; Ogilvie & Ogilvie, 1986). The bulk of the African population is situated in East and southern Africa (Kear & Duplaix-Hall, 1975; Brown *et al.*, 1982; Simmons, 1996). Individual colonies have been estimated at over 1 million birds (e.g. Brown & Root, 1971; Berry, 1972; Brown, 1975; Parker, 1975). The estimated current overall African population is approximately four million (Brown *et al.*, 1982). Of this approximately 55,000 occur in southern Africa (Dodman & Taylor, 1995). Simmons (1996) suggests that numbers have declined by over 20% in recent years, a decline which is in accordance with similar declines in the populations of both species throughout Africa (reviewed in Simmons, 1996) and of flamingos in general worldwide (del Hoyo *et al.*, 1992).

1.6.2 Food and feeding

Flamingos feed in a wide range of shallow water habitats and can be found on coastal shores and lagoons, and inland saline lakes (Allen, 1956; Jenkin, 1957; Brown *et al.*, 1982; Britton *et al.*, 1986). Their uniquely shaped beak is specially 'designed' as an efficient filter feeding mechanism that sieves out the abundant algae and small invertebrates that occur in these waters (Jenkin, 1957;Vareschi, 1978). A number of adaptations to osmotically severe conditions include pre-orbital salt secreting glands (Jenkin, 1957; McFarland, 1959). Flamingos are, therefore, often alone in their exploits of abundant food sources owing to their specific adaptations to life in highly saline environments (Bildstein *et al.*, 1993). By exploiting different food resources both species occupy the same habitat without competition with one another (Brown, 1973; Ogilvie & Ogilvie, 1986).

1.6.3 Breeding and breeding success

Both Greater and Lesser flamingos form large inter-specific breeding colonies. The breeding biology of both species is very similar and well documented in Africa by L.H. Brown (e.g. Brown, 1958, 1973; Brown & Root, 1971; Brown *et al.*, 1972). Mature adults act out an elaborate courtship and breeding in the colony is generally synchronized within each species (Brown & Root, 1971; Brown, 1973; Cezilly & Johnson, 1995). Nests are made from earth and mud and fashioned into mounds of varying heights, depending on water levels (Brown, 1973; Berry, 1972). A single egg is laid and incubated by both adults. Hatching occurs after 28-31 days and approximately three weeks later the chicks congregate to form 'crèches', a strategy that was probably evolved to reduce predation (Baker & Parker, 1979). Chicks remain

in the crèche until fully fledged, 75-90 days after hatching (Brown, 1973, Brown *et al.*, 1982). During this time the parents continue to feed the chicks on 'crop milk' until they can feed themselves and filter feed alongside the adults (Ogilvie & Ogilvie, 1986; Cezilly & Johnson, 1995). Immature birds reach full maturity and begin to breed at the age of between three and five years (Johnson *et al.*, 1993, Cezilly *et al.*, 1996). A vulnerable breeding regime combined with their high sensitivity to disturbance means that successful flamingo breeding is rare (Brown, 1958; 1959; 1975; Broekhuysen, 1975; Simmons, 1996, 2000). Flamingos are, therefore, opportunistic breeders, breeding only intermittently, at a handful of suitably undisturbed sites.

1.6.4 Threatened species

In 'Birds to Watch 2: the World List of Threatened Birds' (Collar *et al.*, 1994) and The IUCN Red List of Threatened Animals (IUCN, 1996), the Lesser flamingo is listed as near threatened across its entire range and both species are listed in the African Eurasian Waterbird Agreement (AEWA, 2000) as populations in decline throughout southern Africa. Their vulnerable status in southern Africa has been attributed, primarily, to the lack of breeding sites and the sensitivity of breeding to both natural and anthropogenic disturbance (Simmons, 1996; Anderson, 2000*a*; *b*). Simmons (1996; 2000) has suggested that a lack of successful breeding at Etosha pan, Namibia and Sua pan, Botswana may have caused greater than a 20% decline of flamingo numbers over the last two decades. Collectively, small wetlands also provide an important habitat network for flamingos that is poorly understood (Breen, 1991; Anderson, 2000*c*). The conservation of flamingos on small ephemeral pans and some perennial wetlands around southern Africa is of concern owing to the lack of formal, effective protection of the majority of these sites (Breen, 1991; Anderson, 2000*c*) that are under increasing threat (Davies & Day, 1986; Allan, 1987; Breen, 1991; Allan *et al,* 1995).

1.7 The Makgadikgadi Pans: site description

1.7.1 Background to its formation

The saltpans of the Makgadikgadi depression are a relict of an immense Quaternary palaeolake that covered most of contemporary northern Botswana (Cooke, 1979*a*; Cooke, 1980; Thomas & Shaw, 1991). Pre-Pleistocene tectonic uplifting, over two million years ago, resulted in an endorheic drainage system and the formation of Lake Palaeo-Makgadikgadi (Du Toit, 1927; Baillieul, 1979; Cooke, 1980). At its peak, some 200,000 years before present (ybp) (Helgren, 1984), a sub-tropical climate and a substantial inflow from the Okavango, Kwando and Upper Zambezi rivers comprised lake input (Grove, 1969; Ebert & Hitchcock, 1978; Cooke, 1980). The result was the formation of one of the largest lakes to have existed in Africa, covering 60,000 to 80,000 km^2 of present-day northern Botswana (Cooke, 1980; Mallick *et al.*, 1981). Further tectonic faulting in the area diverted the flow of the Kwando river east to the Zambezi and stopped the flow of the Okavango River, forming the Okavango delta (Thomas & Shaw, 1991). Following these and other changes in the drainage patterns and with long-term changes in the climate of the region, a succession of lake level changes occurred, and the lake experienced numerous wet and dry periods (Cooke, 1979*b,c* Cooke, 1984; Cooke & Verstappen, 1984). Today remnants of the lake exist in the form of two large salt flats, Ntwetwe and Sua Pan and a large number of smaller pans scattered to the north, west and south, which cover an area of 37,000 km^2 (Cooke, 1979; Shaw, 1988; Thomas & Shaw, 1991). Boundaries delineating old palaeo-Makgadikgadi shorelines exist in the form of escarpments to the East and South and gravel shore beds and large sand dunes to the North and West (Fig 1.1). These shorelines are particularly pronounced at the highest palaeolake level, 940-945 m above sea level (asl) and at a lower lake level 936 m asl (Grey & Cooke, 1977; Cooke, 1979; Cooke, 1980; Shaw & Holmgren, 1997).

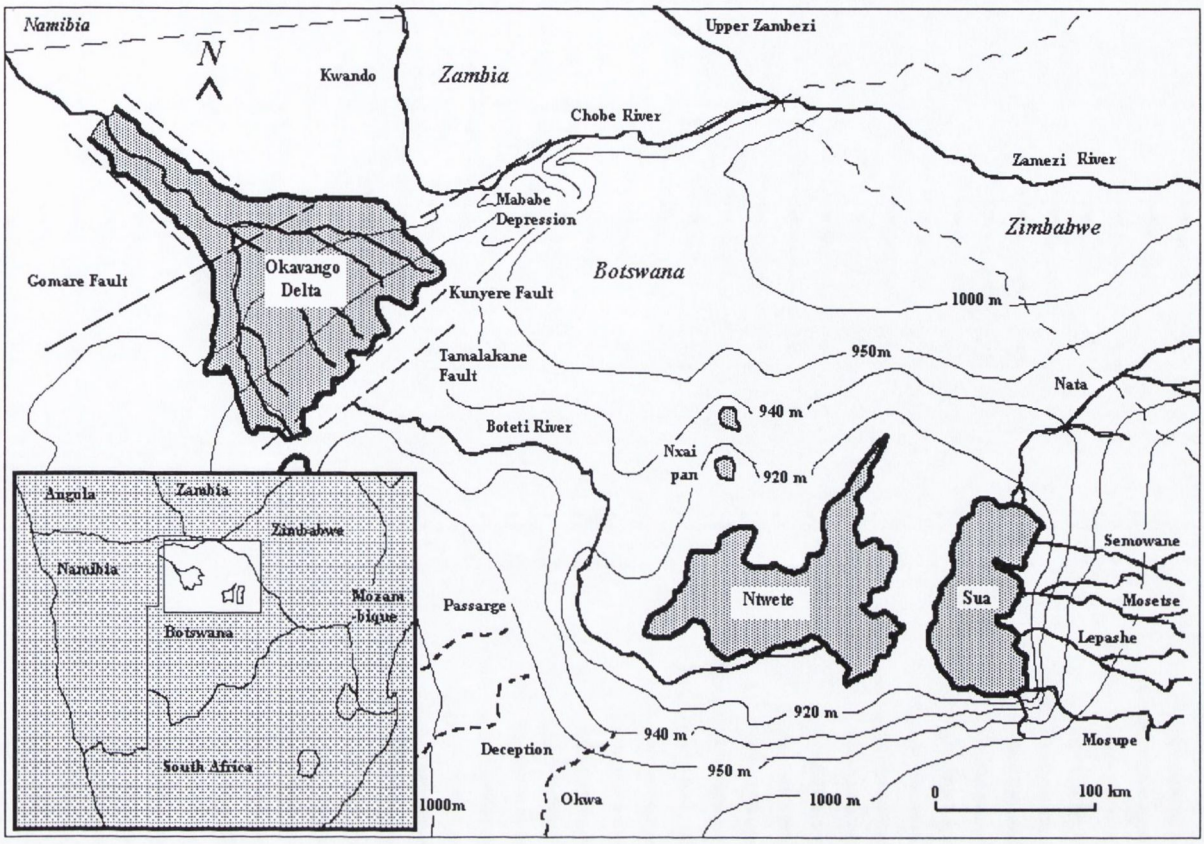


Figure 1.1 Map of northern Botswana showing the Makgadikgadi saltpan complex and the Okavango Delta, with major rivers (———), extinct river valleys (▪▪▪▪▪), and the paleolake Makgadikgadi shore lines (———). Country boarders are also indicated (– – – – –), adapted from Cooke (1979*a*).

Ntwetwe and Sua pan comprise flat surfaces of saline clays and salt efflorescence, beneath which large amounts of saline sediment have been deposited as the lake dried up. These sediments contain large volumes of brine and extend 50-100 m below the surface (Stansfield, 1973; Ebert & Hitchcock, 1978). The geomorphology of these saline playas can be characterised by the deposition and chemical evolution of lacustrine sediments and salts during a wet phase, followed by wind erosion and aeolian transportation of salt and sediment from the pan surface back to the surrounding sand dunes and grasslands during the dry phase (Shaw & Thomas, 1989). Fluctuating groundwater during arid inter-pluvial periods has led to the formation of extensive subsurface paedogenic hardpan layers of calcretes and silcretes. This has led to low porosity in some areas of the main pans and surrounding catchment (Grey, 1976; Shaw *et al.,* 1990). A highly saline groundwater table, however, exists 1-2 m below the

pan surface and influences the hydrological regime of the pans' surface waters (Stansfield, 1973; Ebert & Hitchcock, 1978).

1.7.2 Climate

The climate of the Kalahari occupied by the Makgadikgadi is semi-arid (Schulz, 1972; Tyson, 1986). The year can be separated into a distinct wet and dry season, with an average rainfall of between 400 and 500 mm falling in the wet season/summer (Grove, 1977). A high degree of inter-annual variation in precipitation does, however, occur and the hydrological environment can be characterised by extreme variation in the amount of standing water (Shantz, 1956; Thomas & Shaw, 1991). Owing to the mid-latitude high-pressure belt over the region, a high rate of incident radiation and low relative humidity give rise to warm dry conditions, which predominate for most of the dry season (Schulz, 1972; Tyson, 1986). Under the influence of an equatorial trough called the Inter Tropical Convergence Zone (ITCZ), the climate changes and low pressure and increased convectional activity enhance rainfall during the wet season that occurs between October and April (Cooke, 1979*b*; Thomas & Shaw, 1991). Vossen (1986) defines three different rainfall periods within the wet season, November, January-February and April.

1.7.3 Present status of the Makgadikgadi intermittent wetland

The geomorphologic nature of the Makgadikgadi and its surrounding topography fit the criteria of an endorheic system, as defined by De Martonne & Aufrere (1928). Ntwetwe pan and Sua pan represent the hydrological terminus of an extensive closed drainage basin. The Boteti River channels water from the Okavango system onto Ntwetwe pan. In the present climate, however, the river volume is barely sufficient to reach the pan before it is lost through ground water infiltration and evaporation (Cooke, 1980). Other drainage lines, like the Okwa and Nunga fossil rivers, to the southwest and north of Ntwetwe, do not function at all under the current climatic regime (Thomas & Shaw, 1991). Sua pan covers approximately 3700 km^2 and with a sump level of 890-900 m abs, is the lowest part of the basin (Ebert & Hitchcock, 1978; Cooke, 1979*a*). It receives water from a large catchment via five rivers, the Nata, Semowane, Mosetse, Lepashe and Mosope rivers. The combined inflow from these rivers along with direct precipitation and local runoff is enough to flood large parts of the pan surface in years of average rainfall. The duration of the wet phase depends on the magnitude of, and temporal relations between, water income and water loss (Ebert & Hitchcock, 1978;

Cooke, 1979*a*; Shaw, 1994). In years of exceptional rainfall, for example, flooding can cover the whole pan and last throughout the dry season.

1.7.4 Flora and fauna

Warm, saline and nutrient rich conditions are conducive to high biotic productivity, yet very little is known about the biota of these waters and up until now little research has been conducted on the limnology of the Makgadikgadi. This is highlighted by the fact that it has been omitted or given scant recognition in limnological reviews on inland waters of southern Africa and/or Africa, (Ashton & Schoeman, 1983; Livingstone & Melack, 1984; Mepham, 1987; Allanson *et al.*, 1990; Day, 1993; Talling & Lemoalle, 1998). An early expedition by the Rhodesian Schools Exploration Society, resulted in some taxonomic data on the invertebrate fauna of the Nata River and the sump area of Sua pan (Eccles, undated). Seaman *et al.* (1991) subsequently republished this data on the fauna of the Makgadikgadi when comparing it with faunal data from other inland waters of southern Africa. Since then only a single paper on the anostracans of Botswana has been published, which included three species that live on and near Sua Pan (Brendonck & Riddoch, 1997). The lack of knowledge about the limnology of the Makgadikgadi is surprising considering it is one of the largest inland saline lakes on the sub-continent and one of extreme importance for both intra-African and Palaearctic migrant bird species (Coulson *et al.*, 1991; Liversedge *et al.*, 1989). Approximately 130 bird species have been reported in the area around the Nata river delta (Mundy & Borello, 1990), including many listed as protected and endangered species (Collar *et al.*, 1994; AEWA, 2000) and one of the largest congregations of flamingos in southern Africa (Hancock, 1990; Simmons, 1996; 2000). Protection of the Makgadikgadi wetland ecosystem comes in the form of small areas of local and private conservation areas, the Nata Sanctuary established in 1988 (a community based project that covers ~ 200 km^2 of the pan around the Nata River delta and its surrounding grasslands) and the Botswana Ash (Pty.) Ltd. Conservation Area established in 1991, which covers some 200 km^2 of pan in the north of Sua pan. Much of Ntwetwe pan and Sua pan lacks any national or international conservation and has remained protected only through its isolation and inaccessibility. The entire Makgadikgadi saltpan complex has been proposed as Botswana's second Ramsar site as a site of international importance as it satisfies the conditions of importance to waterbirds (NCSA, 2000).

1.8 Thesis outline

A lack of baseline data on the physico-chemical factors controlling organic production as well as the type and production of, and inter-relationships among, the biological components of the Makgadikgadi wetland ecosystem make it difficult to:

(a) identify any deleterious affects from anthropogenic activities because there is no background data with which to compare possible trends from disturbance;

(a) draw up effective management strategies to prevent such disturbance because the important factors controlling biological production and the interactions among the biota of the ecosystem are unknown; or

(b) increase our understanding about the factors controlling food availability and breeding conditions of the Greater and Lesser flamingo populations because their food type and availability is unknown in relation to breeding occurrence and success on Sua.

With that in mind, this study attempted to provide an improved understanding of the limnology of the Makgadikgadi and the ecology of its biological components to facilitate future monitoring and management of the pans, and ensure its integrity and conservation status as one of only a handful of flamingo breeding sites in Africa.

Owing to the logistical constraints of carrying out research on such an immense and largely inaccessible wetland complex, research efforts were concentrated on the temporary lakes of Sua pan during the course of three wet seasons, from October 1998 to July 2001. The thesis is presented as five main chapters, each representing a major component of the physico-chemical and biological characteristics of Sua pan's ecosystem.

Chapter 2 attempts to record the dynamic hydrology of Sua pans over three wet seasons and the important factors contributing to the hydrology of Sua pans by comparing some of the major sources of water input. Daily meteorological data on rainfall and evaporation rates around Sua pan and in the catchment areas of the inflowing rivers were used from various government gauging stations during the three wet seasons. Together with river discharge data, collected from a government gauging station on the Nata River, total inputs of water onto the

three basins of Sua pan were estimated for each season. Flood periods were estimated from evaporation rates and corresponding flood areas were determined from satellite images of the pan during the second and third wet seasons, using image-processing software.

Chapter 3 concerns water chemistry on Sua pan and attempts to determine the origin, composition and variable concentrations of dissolved ions and nutrients in the floodwaters. Conductivity measurements were made of water from the three basins during the second and third wet seasons. Analyses of the ionic composition of flood waters, in monthly samples from each of the three basins, during the second season, was determined in US laboratories, while total and dissolved phosphorus and total nitrogen concentrations were analysed from monthly samples during the third wet season. Temporal fluxes in both salinity and nutrient concentrations and their potential influences on biological composition and production are discussed.

Chapter 4 concerns the primary producers and attempts are made to identify and quantify their community composition and estimate primary production using P:B ratios from the literature. In order to do this, data were collected from weekly phytoplankton and epipelic periphyton samples, taken from each basin during the second and third wet seasons. The primary controlling factors of primary production are discussed in relation to the changes in abundance and production throughout the flood periods.

Chapter 5 concerns the crustacean community and secondary productivity. Identification and abundance estimates are reported, based on weekly samples from each basin using two sampling techniques, during the second and third wet seasons. Length-weight relationships were calculated for the most abundant species and together with length frequency analyses weekly biomass estimates were calculated from both seasons data. Life history data were also collected for two anostracan species in order to calculate their production during the flood periods. Production for the other common species was estimated using P:B ratios from the literature;

Finally, Chapter 6 outlines Greater and Lesser flamingo population numbers and breeding success, monitored from the air during all three seasons. Biomass densities and breeding productivity for both populations was calculated and assessed in terms of flamingo food

requirements and compared with the availability of food (crustaceans for Greater flamingo and algae for Lesser flamingo) on Sua pan. The significance of Sua pan as one of the most important breeding sites in Africa and the potential control of food availability on breeding success are discussed.

Chapter 2

Hydrology and flood period

2.1 Introduction

2.1.1 Topographical and hydro-morphological background

Sua pan is a large drainage terminal sink that covers approximately 3,700 km^2 (Ebert & Hitchcock, 1978; Cooke, 1979*a*). It can be divided into three hydrologically separate basins, the north, middle and south basins, separated by two sand spits that protrude from the eastern shoreline (Fig 2.1). Palaeo-hydrological budgets suggest that the Makgadikgadi basin was once filled with some 50 km^3 of water. This would have required an average annual rainfall of approximately 1500 mm and a large river discharge from a number of big rivers, including the Upper Zambezi and Okavango (Grove, 1969; Ebert & Hitchcock, 1978; Cooke, 1979*a*,*b*). Today, inputs are small compared with the size of the pans. For periods during the wet season, five rivers flow intermittently from East to West, in a dendritic drainage pattern, and fill parts of Sua Pan's gently slopping basins. These inflowing rivers and their catchments can be divided according to their connection with the three separate basins (Table 2.1).

Table 2.1 Rivers and drainage basins of Sua Pan

Pan Basin	River
North	Nata and Semowane
Middle	Mosetse
South	Lepashe and Mosope

The area of flooding (Fig. 2.1) varies between seasons depending on the amount and intensity of rainfall. In years of high rainfall, the combined input from precipitation and inflowing rivers is sufficient to fill varying proportions of all three basins (Ebert & Hitchcock, 1978; Cooke, 1979*a*,*c*). Owing to a gentle slopping gradient from West to East, the eastern parts of each basin are the first to flood and last to dry out. The north basin sump is the deepest part of the pan, estimated at 890 m above sea level (asl), and is flooded every year (Cooke, 1979*a*). A

rainfall threshold of 20 mm has been set as the minimum amount of rainfall needed to produce standing waters in temporary wetlands, in other parts of southern Africa (Meintjes *et al.*, 1994). Variations in the size of temporary lakes occur within seasons owing to the constant change in water balance between rapid input, from precipitation and runoff, and rapid loss by evaporation.

By far the largest of Sua pan's inflowing rivers is the Nata River, which flows into the north basin. It has a large catchment of 22,500 km^2 (Dept. of Water Affairs, Botswana) that extends into southwestern Zimbabwe. The upper part of the catchment lies in an area with a mean annual rainfall of 500-600 mm, 100-200 mm more than the mean for the lower part of the catchment (Schultz, 1972). Its size and contribution to the flooding of the pan have been gauged in the past and it is the only river for which detailed historical records of discharge exist. Records of flows, measured at a gauging station on the Nata Bridge (Fig 2.1) between 1969-1996, give an annual mean of 143.9 mcm (10^6 m^3), ranging from a minimum of 0.4 mcm (1994-95) to a maximum of 805.7 mcm (1971-72) (DWA, 1991). Records for nine of the interim years, however, are missing. The correlation between Nata river flow and point daily rainfall data from Nata town is low owing to the size of the catchment and the spatial variability of rainfall events (Ecosurv, 1993).

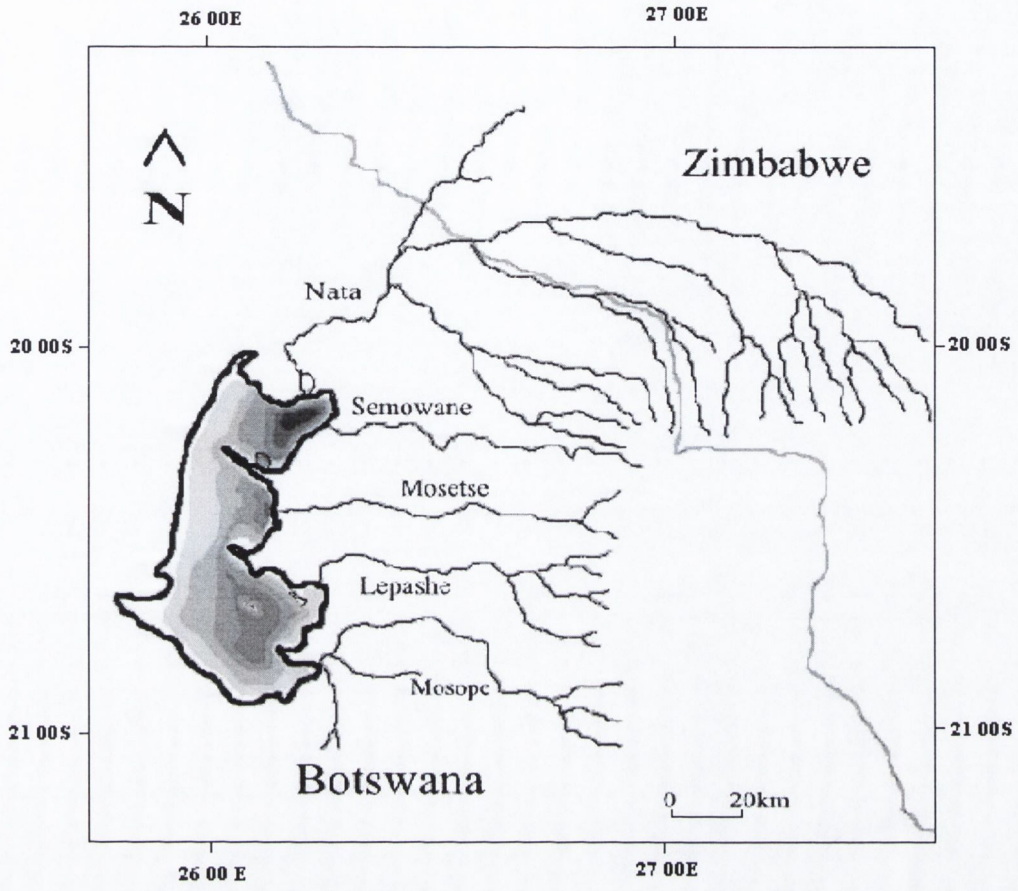


Figure 2.1 Map of Sua Pan showing the inflowing rivers Nata, Semowane, Mosetse, Lepashe and Mosope and the flooding patterns of the North, Middle and South basins at different levels of flooding. The small area encircled in the north basin represents solar ponds belonging to the soda ash production plant, Botswana Ash (Pty) Ltd.

Discharge data for the other rivers are, however, sparse and their total volumetric contribution to Sua Pan is not known. Their individual catchment areas are, however, considerably smaller than the Nata river catchment. Rainfall-runoff relationships for small rivers in semi-arid areas are not easily defined and tend to be rapid and of short duration (Yair & Lavee, 1985; Shaw, 1994). Mean annual runoff for the Mosetse has been calculated as 26.4 mcm, although no source for this figure was given (Syratt & Martin, 1985). An absence of adequate data on smaller river discharge, together with the extreme spatial and temporal variability of the factors controlling river discharge in semi-arid areas, makes it very difficult to predict

probable flow and requires continuous records (Verma, 1979; Doran, 1979). Furthermore, models of short-term river discharge on these types of rivers tend to be inaccurate and have limited theoretical and practical value (Yair & Lavee, 1985). Satisfactory estimates of gross annual water yield from a catchment can, however, be accomplished using relationships between annual rainfall and runoff (Shaw, 1994). The proportion of water gained from the catchment via rivers can be evaluated by comparing the total rainfall volume over the catchment with the total annual discharge from the respective inflowing rivers (Shaw, 1994). The difference will represent the amount of water lost in the catchment to ground water and evapotranspiration.

Catchment size, soil porosity, vegetation cover and gradient influence the temporal dynamics of the rainfall-runoff relationship (Yair & Lavee, 1985; Shaw, 1994). The upper eastern boundary of the Makgadikgadi river catchments are dominated by major escarpments of Karoo sandstones and Basalts, that define the shore of the ancient palaeolake and average 945m asl (Stansfield, 1973; Thomas & Shaw, 1991). Relief difference to the basin sump averages 50 m (Cooke, 1979*a*; Ecosurv, 1993). Some parts of the eastern extremities, however, reach as high as 300 m above sump level (Mepham, 1987). The soils of the catchments, characterised by their formation on the Kalahari sand and their close relationship with the underlying geology, are described as predominantly arenosols with some poorly drained calcisols, luvisols, vertisols and gleysols (Sims, 1981; Thomas & Shaw, 1991; Thompson, 1965). Most of the soils in the area, particularly those close to the pan, have calcrete layers at shallow or moderate depths. Vegetation cover in the catchment is dominated by mixed Mopane tree (*Colophospermum mopane*), scrub woodland and bush savannah, with some halophilic grassland savannah close to the pans (Werger, 1978; Weare & Yalala, 1971).

2.1.2 The water balance on Sua pan

Standing water input on Sua pan comes from direct precipitation, river inflow and ground water seepage. Water loss occurs, predominantly, through evaporation, with some loss to the ground water (Thomas & Shaw, 1991; Ecosurv, 1993). Standing water can be represented by the equation;

$$Ip + Ir + Ig = Le + Lg$$

where *Ip*, *Ir* and *Ig* are, respectively, inputs from precipitation, river inflow and groundwater seepage and *Le* and *Lg* are losses through, respectively, evaporation and ground water seepage (Langbein, 1961).

The predominant factor controlling the formation of standing water on Sua pan is, therefore, rainfall. Mean annual rainfall for the Makgadikgadi area is estimated at between 400-500 mm, falling mainly in the high rainfall months of January and February (Schulze, 1972; Tyson, 1986; DWA, 1991). Large inter-annual fluctuations are characteristic of the climate (Schulze, 1972) and the extent of annual water gain is, therefore, highly variable. Mean annual rainfall on Sua pan is 493 mm, ranging between 221 and 753 mm (Dept. of Meteorological Services, Botswana). Rainfall type also influences water input. Owing to the effects of the inter-tropical Convergence Zone (ITCZ), wet season rainfall events occur, predominantly, in the form of late afternoon convective thunderstorms (Longley, 1976). High intensity storm showers make up approximately 20% of rainfall events (Cooke, 1979*c*) and are important contributors to river discharge (Shaw, 1994).

The hydrology of closed lake basins in semi-arid regions is also influenced by ground water contributions (Thomas, 1989). It is likely that the Makgadikgadi pans act as a terminal sink for ground water from the middle Kalahari (Thomas, 1989; Thomas & Shaw, 1991). Evidence indicating its importance in terms of contributing to Sua pans surface water is, however, absent in the literature.

The amount of water loss by evaporation from a free water surface, measured by the Department of Water Affairs using "class A" pans, is approximately 3000 mm in this part of the Kalahari. This has been attributed to high solar radiance and temperatures that range

between mean daily maximums of 25^0C during the winter months, and 35^0C in the summer (Schulze, 1972; Tyson, 1986). Mean monthly PET exceeds rainfall during all months of the year and, unlike in temperate regions, where evaporative loss occurs, predominantly, as evapo-transpiration from the catchment, loss by evaporation in semi-arid regions occurs mainly from lake surfaces. Rapid water movement from the catchment to the lake ensures low evapo-transpiration rates in the catchment. Evaporation rates from the surface of a lake are directly linked to lake area, depth and relative proportions of catchment and lake area, which, in turn, directly affect the period of flooding (Hartland-Rowe, 1972; Shaw, 1994). Assuming rapid discharge from the catchment into the lake, the presence of water and the extent of flooding in a closed basin were expressed by the equation;

$$(P_r\text{-}E_v) + ((A^1\text{-}A)/A)\ (P_r^1\text{-}E_v^1) > 0$$

where P_r is mean precipitation over the lake surface, P_r^1 the mean precipitation over the rest of the drainage basin, E_v the mean evaporation from the lake surface, E_v^1 the mean evaporation from the rest of the drainage basin, A the area of the lake and A^1 the area of the drainage basin including the lake (Shaw, 1994). The area of the lake in proportion to the catchment area has, therefore, a major influence on the presence of water and its rate of change (Hutchinson, 1957).

2.2 Materials and methods

2.2.1 Rainfall and evaporation

2.2.1.1 Annual rainfall and evaporation

Rainfall data for the Sua Pan area were collected at a Department of Meteorological Services station on the edge of Sua Pan (Figure 2.2), using a standard rain gauge. Depths (mm) of rainfall for a 24 hr period were recorded at 8 am every day. Daily maximum and minimum temperatures were also recorded at the Met. service station and mean maximum and minimum temperatures were calculated for each month.

Evaporation rates were also estimated and recorded by the DMS at the meteorological station, using a Class A Pan. The pan, 1.21 m in diameter and 25.5 cm deep, contained water that was kept 50 mm from the top rim. The level of water in the pan, measured with an adjustable 'hook gauge', was recorded at 8 am every day. The difference in the level after each 24 hr period was estimated as the total loss of water by evaporation for that period. Direct sunlight can heat up the side of the pan and exaggerate evaporation, although a wire mesh, placed over the pan to prevent birds and animals from drinking the water, was considered to balance estimates by reducing incident radiation.

Rainfall and evaporation rates were used to calculate net loss or gain of water on a daily bases throughout the three seasons 1998-99, 1999-2000 and 2000-2001.

Figure 2.2 Map of Sua pan and its catchment area, showing the weather stations and river gauging stations. The grey squares represent rainfall data collection sites and the black circles represent the positions on three rivers where discharge measurements were recorded. Initials on the map correspond to the following sites; Sua Pan (S), Semowane river (SM), and villages; Mosetse (M), Dukwi (D), Nata (N), Sepako (SP), Tutume (T), Senete (S), Nkange (N), Maitengwe (MW), Goshwe (G), Lepashe (L), Matsitama (MA), Mokubilo (MK) and Mosu (MU).

2.2.1.2 Catchment rainfall

Rainfall data in the river catchments was collected from several gauging stations in each catchment area, using standard rain gauges (Fig 2.2). Monthly rainfall totals for each of the three wet seasons were collected by DMS from school and police station records (Table 2.2). Although some degree of error existed in these data sets owing to omissions of recordings on

Sundays and public holidays and the density network of gauging stations was inadequate to account for the full variation in rainfall across the catchment, the compiled data were deemed a reasonable account of total monthly rainfall in the absence of DMS recording stations in these areas.

Table 2.2 Rainfall data collection stations in each river catchment

River catchment	Gauging stations (Villages)
Nata	Nata, Sepako, Senete, Nkange, Maitengwe, Tutume & Goshwe
Semowane	Sua Pan, Dukwi & Nata
Mosetse	Tutume, Mosetse, Dukwe & Sua Pan
Lepashe	Matsitama, Lepashe
Mosupe	Matsitama, Lepashe, Mosu & Mokubilo

Areal monthly rainfall for each catchment was calculated by averaging the data from all stations in each catchment. Data from some stations in neighbouring catchments were pooled with those in catchments with one or two stations, in order to calculate an average for the area.

2.2.2 River discharge

2.2.2.1 Nata river discharge and depth

Discharge measurements of the Nata river were made on a daily bases by the Department of Water Affairs (DWA), at Nata Bridge (Fig 2.2). Discharge (Q) was estimated using the velocity-area method (Shaw, 1994):

$$Q\ (m^3s^{-1}) = \sum VA$$

where V is the velocity of a river section, measured in m s^{-1} and A is the area in m^2. Velocity was measured with a propeller current meter at 12- 20 intervals across the river and at 0.2 m and 0.8 m below the surface, or 0.6 m when the river was less than 1 m deep. The mean

velocity of the intervals was calculated and multiplied by their corresponding sub-areas of the river cross section. A was estimated at each sub area by multiplying the horizontal distance between two successive measuring points by the depth of water. The sum of VA for each sub-area gave the total river discharge. Water level was also measured twice daily, at 08:00 and 14:00 hours, using a staff gauge.

Maximum potential yield of the catchment was calculated by converting mean rainfall over the catchment into a total for the entire catchment by:

$$Q_e = A^1 \text{ x } P_r^1$$

Where Q_e is the expected river flow in m^3, A^1 the area of the river catchment and P_r^1 the mean net rainfall (rainfall less evaporation) over the catchment area. This method assumes that rainfall and topography are uniform over the catchment and depends crucially on the quality of the data collected at the catchment gauging stations (Shaw, 1994). Expected discharge and discharge measured by DWA were compared to evaluate a rainfall-runoff relationship for each season and express measured river discharge as a percentage of the total volume of water falling onto the catchment.

2.2.2.2 Calculating river discharge for the other rivers

River discharge on the Mosetse and Mosope rivers were measured at different depths on a number of occasions. Q was measured using a pygmy flow meter to calculate velocity according to the velocity-area method, as above. Depth was also measured on each river using a DWA staff gauge situated on a bank of each river. Only a small number of discharge measurements were taken from each river when depths were low, owing to the dangerous flash flood nature of discharge in these rivers. The data collected was, therefore, deemed insufficient to establish any reliable stage-discharge relationship in order to predict discharge from river depth records. Runoff volume for each river was estimated by predicting annual rainfall-runoff relationships from catchment size and average areal rainfall for each catchment. Catchment area for each river was calculated from geo-referenced government maps of the areas (scale of 1:250,000). Total rainfall over each catchment was calculated by multiplying the mean annual rainfall for each catchment by their respective catchment areas. Estimates of the proportion of catchment rainfall entering the pan as river discharge was calculated using the proportional discharge ratio from the Nata River.

2.2.3. Temporary lake size and life span

2.2.3.1 Calculating total water input

Net daily rainfall measured at Sua pan, was converted into total volumes falling over the north, middle and south basins. ArcView GIS 3.2® software was used to calculate the basin areas from geo-referenced Landsat satellite images of Sua pan. Direct input from precipitation was combined with annual discharge onto each basin by their respective rivers and, assuming negligible input from ground water seepage, the total annual input of water into each basin was calculated for three seasons.

Mean daily evaporation rates for each month were calculated and used to predict the loss of water from the pan. Combining the inputs of water onto the pan and subtracting the mean daily evaporation rates, on a daily basis, calculated the theoretical potential life span of each temporary lake by:

$$(P + Q) / (E_d \text{ x } A) = L$$

where P (mcm) is the net annual input of water onto the pan by direct precipitation, Q (mcm) the annual river discharge into the pan, E_d (mm) the mean daily evaporation rate for the wet season, A (km^2) the area of the basin in question and L the lifespan of the lake in days. These calculations were then compared with the actual time it took for each basin to dry up after each flooding event.

2.2.3.2 Flood area

The Jet Propulsion Laboratory, NASA, provided satellite images of Sua pan, taken from the MODIS instrument on NASAs TERRA satellite during the 1999-2000 and 2000-2001 wet seasons. The proportional flood area on each image was estimated using ArcView GIS 3.2® software. Flood area was multiplied by average water depth, taken with a meter stick, at five random sites in each basin during phytoplankton and crustacean sampling (Chapter 4 and 5), to calculate lake volume for Sua pan at the time each image was taken.

2.3 Results

2.3.1 Rainfall and evaporation

2.3.1.1 Annual rainfall

Total annual rainfall for Sua Pan varied considerably over the three seasons. All of the major rainfall events measured occurred during the wet seasons, from October to April, although there were some showers in June 2000. Total estimated rainfall was 442 mm in the 1998-1999 wet season, 851 mm in the 1999-2000 wet season, and 348 mm, for the 2000-2001 wet seasons. Although the majority of rainfall occurred in the months of December to March, monthly rainfall amounts varied from season to season and (Fig. 2.3).

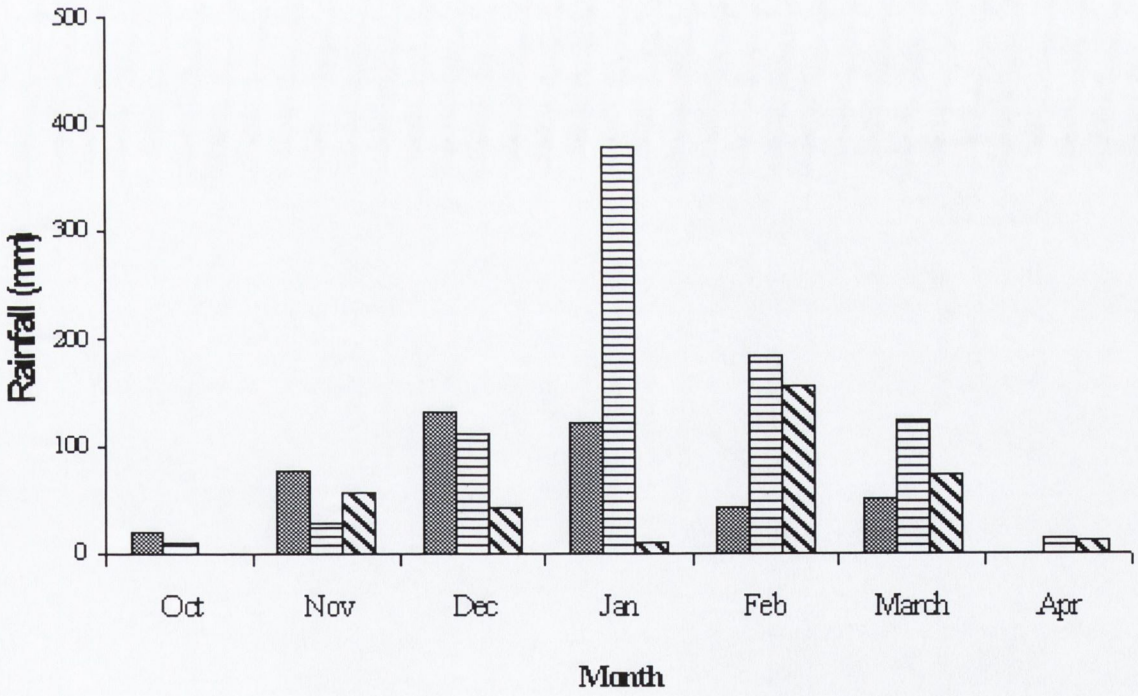


Figure 2.3 Total monthly rainfall over three wet seasons, 1998-1999 ▩, 1999-2000 ▤ and 2000-2001 ▨ , recorded at the Department of Meteorology, Sua Pan station.

2.3.1.2 Daily temperatures

Mean maximum and minimum daily temperatures varied according to season (Fig. 2.4). Recorded maximum temperatures were highest in the early summer months (38-41°C), from October to December, and decreased to between 22 and 24°C in mid winter (June to August). The lowest recorded minimum temperatures of 4-7°C were recorded in the months of June and July.

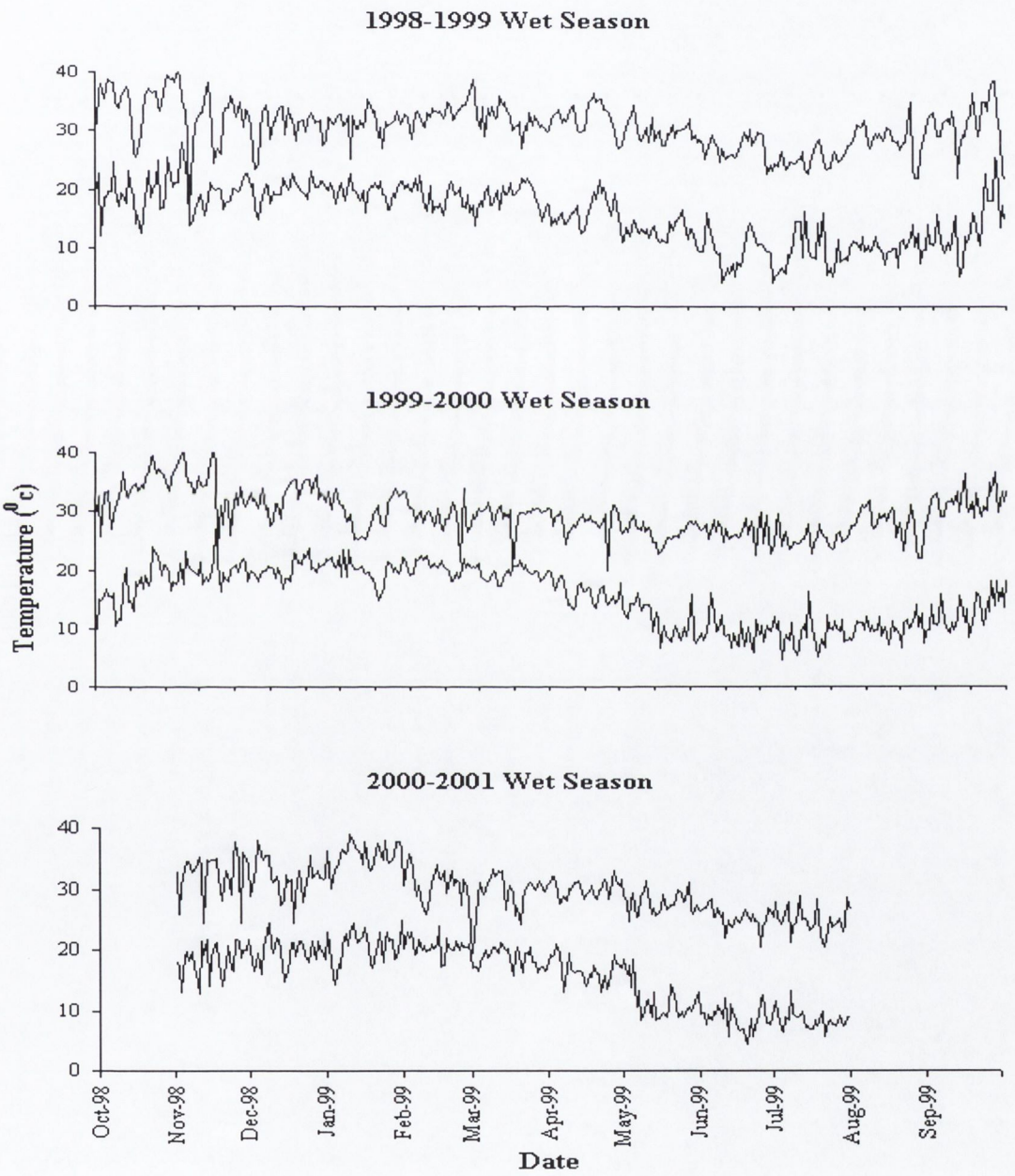


Figure 2.4 Maximum and minimum daily temperatures during the 1998-1999, 1999-2000 and 2000-2001 wet seasons. Data was incomplete for the 2000-2001 wet season.

Average maximum temperatures ranged from an average of 35 °C in October 1998 to 25 °C in July 1999 and 34 °C in October 1999 to 25.4 °C in July 2000 (Fig. 2.5). With an absence of records from October 2000, the recorded monthly maximum during the 2000-2001 wet season, of 33 °C, occurred in November 2000 and the season's minimum of 25 °C occurred, again, in July of 2001.

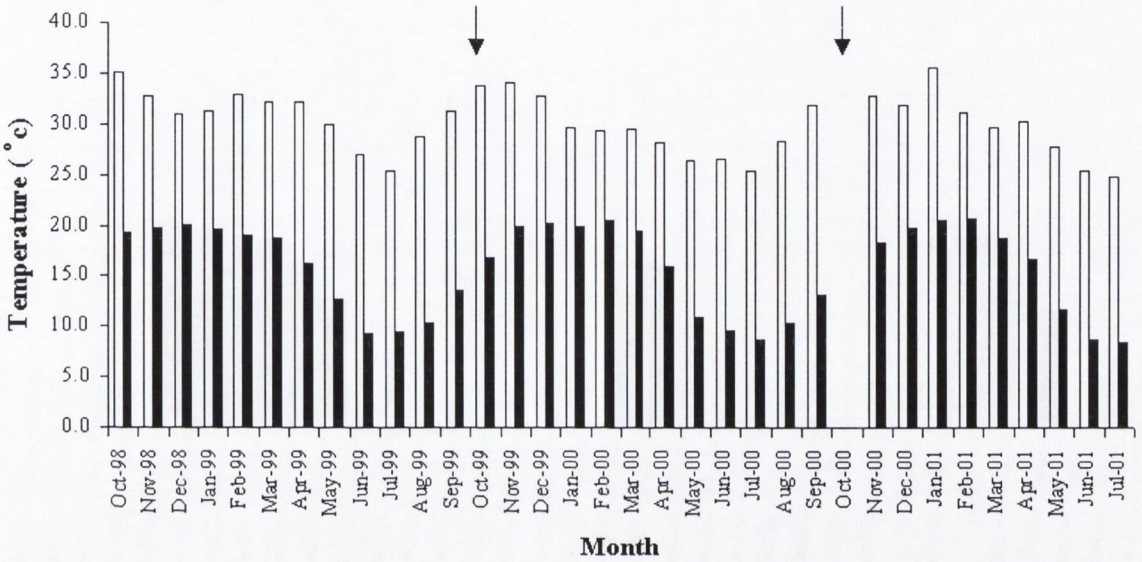


Figure 2.5 Average maximum (white bars) and minimum (black bars) monthly temperatures for the 1998-1999, 1999-2000 and 2000-2001 wet seasons. Arrows indicate the start of the 1999-2000 and 2000-2001 wet seasons.

2.3.1.3 Potential evapo-transpiration

Annual potential evapo-transpiration (PET) was calculated using the combined daily evaporation rates for the year. Annual PET was 2925, 2670 and 2822 mm for the 1998-99, 1999-2000 and 2000-2001 seasons, respectively, or an overall mean of 2806 mm. Daily evaporation rates varied according to season and ranged from 3.1 mm d^{-1} on cold, cloudy days in winter, to maximum recorded rates of 20 mm d^{-1} on very hot, windy days in the summer. Monthly evaporation rates were highest at the beginning of the wet season and were lowest during the colder winter months of May, June and July (Fig. 2.6).

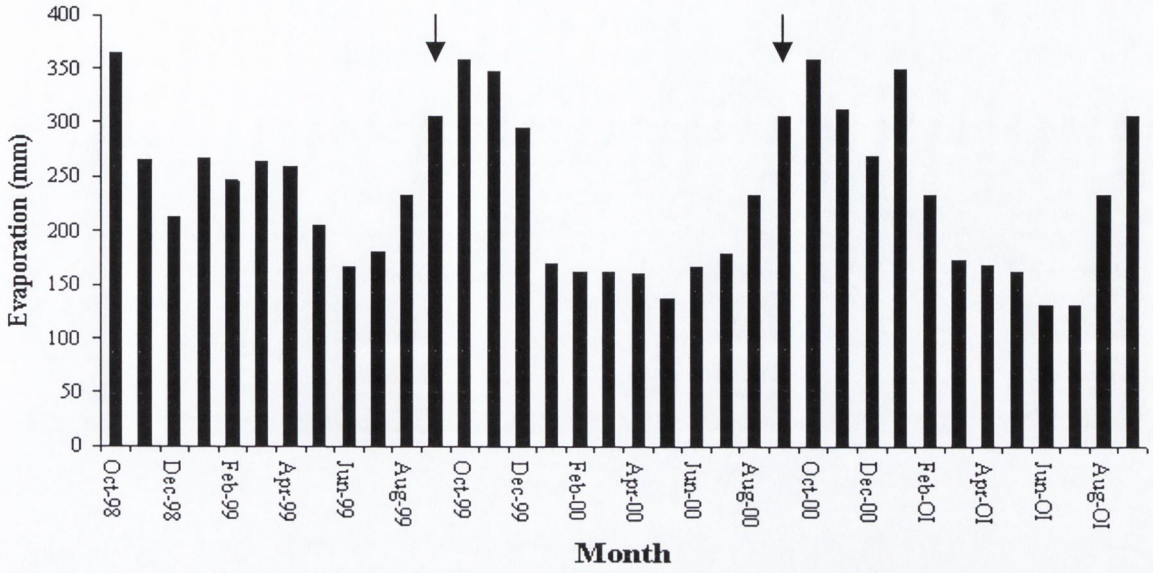


Figure 2.6 Monthly evaporation rates over three years from October 1998 to September 2001, calculated from daily evaporation rates recorded by the Department of Meteorology Services, at Sua Pan. Arrows demarcate the beginning of the 1999-2000 and 2000-2001 wet seasons.

2.3.1.4 Net rainfall

High temperatures and evapo-transpiration meant that much of the rainfall that fell on Sua pan disappeared quickly. Only high intensity, persistent rain, produced a net surplus and contributed to standing water on the pan (Fig 2.7). During the 1998-1999 wet season, net rainfall intensity was relatively moderate and occurred frequently between November 1998 and February 1999. Monthly net rainfall totals were estimated to be 40, 83, 90 and 53 mm for, respectively, November, December, January and February. Rainfall intensity during the 1999-2000 wet season was considerably higher, particularly in January and February, and heavy rainfall events were frequent throughout the season. Monthly totals were 33, 334, 131, and 88 mm for, respectively, December, January, February, and March of that season. Rainfall intensity and frequency were considerably lower during the 2000-2001 wet season and net surplus rainfall was low in comparison with the previous two seasons. Recorded totals for the months of November, December, February and March of that season were, respectively, 12, 7, 87, and 53 mm.

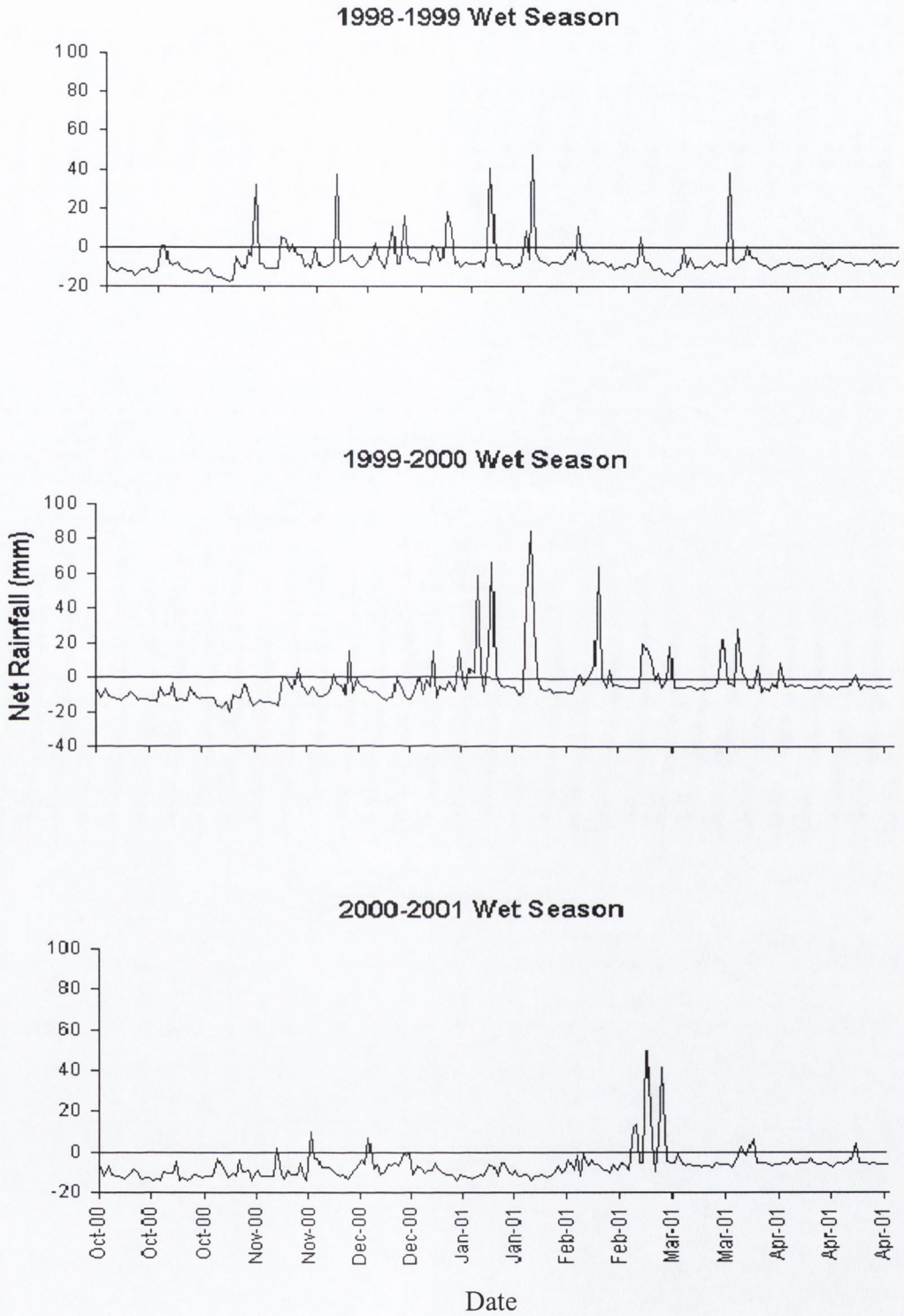


Figure 2.7 Total net rainfall at Sua Pan over three wet seasons. Rainfall above the line at 0 represents water gain on the pan.

2.3.1.5 Rainfall in the catchments

Annual rainfall in the river catchments varied among gauging stations, suggesting localised variation in rainfall. A mean value with standard deviation (SD) for each river catchment was calculated during each wet season, where n (number of data points) was 7, 3, 4, 2, and 4 for, respectively, the Nata, Semowane, Mosetse, Lepashe and Mosope rivers (Table 2.3 & Fig. 2.8). Rainfall varied among the catchments and ranged from 311 to 497.2 mm during the 1998-1999 season, 818 to 869.6 mm during the 1999-2000 season, and 280.5 to 416.5 mm during the 2000-2001 season.

Table 2.3 Mean annual rainfall (mm) for river catchments during three wet seasons, calculated from a number of gauging stations in each catchment (n). Variation around the mean annual rainfall for each catchment is expressed as standard deviation (SD).

River Catchment		1998-1999 Mean ± SD	1999-2000 Mean ± SD	2000-2001 Mean ± SD
Nata	n = 7	311 ± 81	820 ± 201	416.5 ± 127
Semowane	n = 3	408 ± 127	839 ± 96	322 ± 49
Mosetse	n = 4	497 ± 5	818 ± 82	327 ± 44
Lepashe	n = 2	462 ± 45	870 ± 92	281 ± 69
Mosope	n = 4	439 ± 67	868 ± 73	359 ± 113

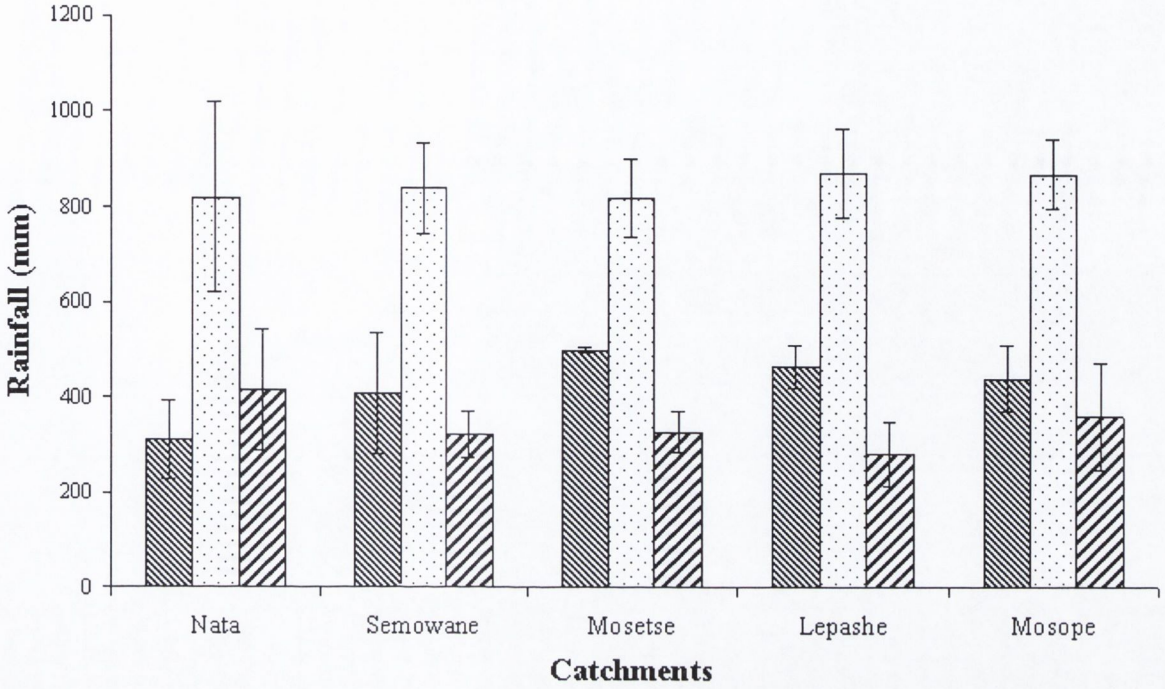


Figure 2.8 Mean annual rainfall in the catchments of Sua pans inflowing rivers, during the 1998-1999 ▨, 1999-2000 ⊡, and 2000-2001 ▨ wet seasons, compiled by the Department of Meteorological Services, Botswana. Error bars represent the standard deviation around mean catchment rainfall (n = 7, 3, 4, 2, & 4 for, respectively, the Nata, Semowane, Mosetse, Lepashe & Mosope rivers).

2.3.2 River discharge onto Sua Pan

2.3.2.1 Nata River

The Nata River was dry for most of the year, but discharge did occur during the months of high rainfall in the wet seasons (Fig. 2.9). Annual totals of river discharge were 202.63 m^3 10^6 (mcm), 542.6 mcm and 67.35 mcm for, respectively, the 1998-1999, 1999-2000 and 2000-2001 wet seasons. River depth increased and decreased with discharge volume (Fig. 2.10). Pearson product moment correlations showed a highly significant positive relationship between water levels and discharge during the 1999-2000 wet season ($r = 0.94$, n = 32, $P \leq 0.001$) and the 2000-2001 wet season ($r = 0.98$, n = 47, $P \leq 0.001$).

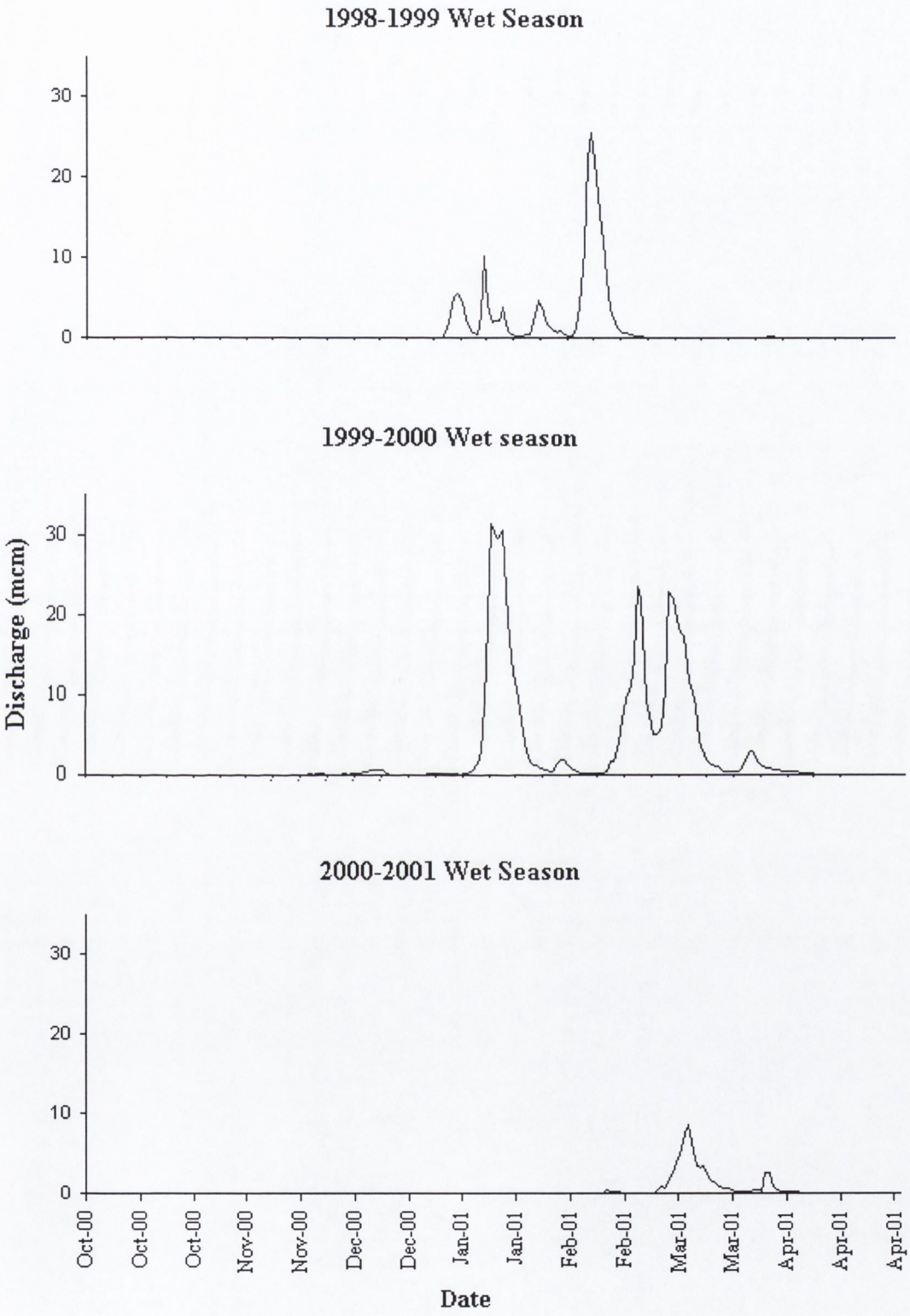


Figure 2.9 Daily discharge of the Nata River during three wet seasons, 1998-99, 1999-2000 and 2000-01.

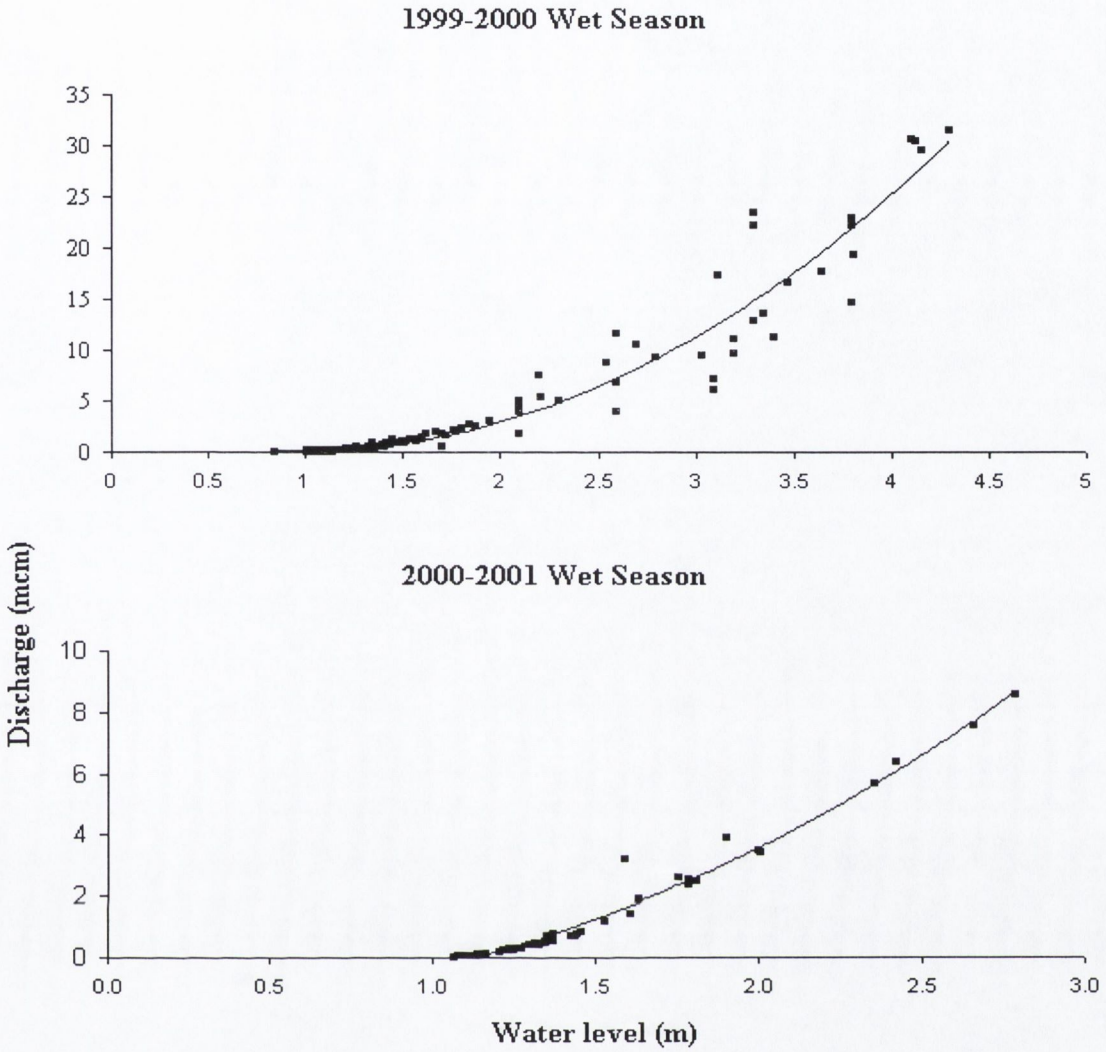


Figure 2.10 Relationship between water levels and discharge of the Nata River during the 1999-2000 and 2000-2001 wet seasons. Log-log linear regression equations were ln Q = 4.25 ln D – 0.974 (r^2 = 0.93 %, F-ratio = 1630, n = 32, $P \leq 0.0001$) for the 1999-2000 wet season and ln Q = 5.68 ln D – 1.16 (r^2 = 0.89, F-ratio = 374, n = 47, $P \leq 0.0001$) for the 2000-2001 wet season.

No significant correlation was found between Nata River flow and rainfall in the catchment (Fig. 2.11). A relatively large lag period before the river began to flow was observed after the first rains, but the response became more rapid later in the season.

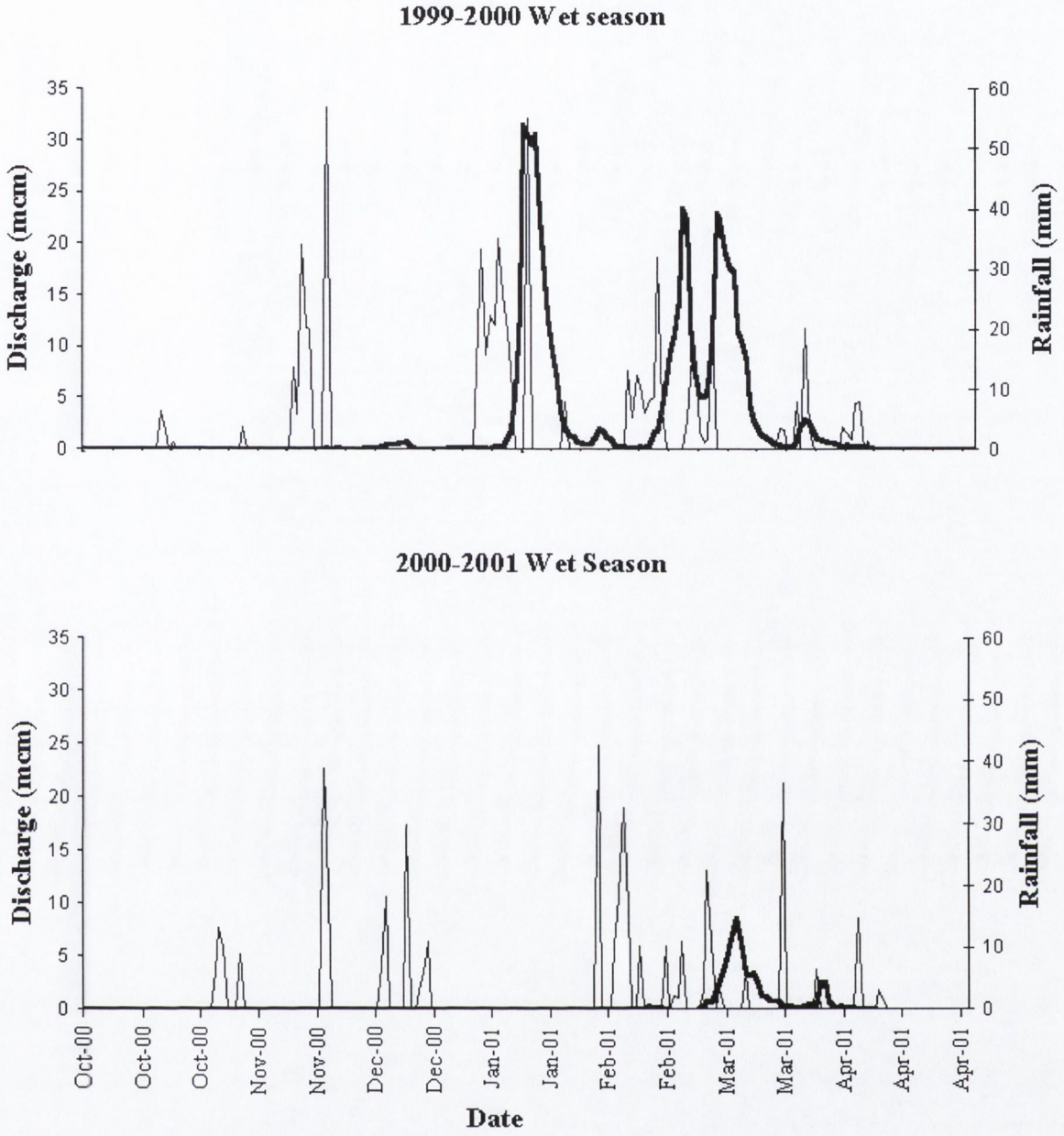


Figure 2.11 Daily discharge (heavy line) and catchment rainfall (faint line) for the Nata River during the 1999-2000 and 2000-2001 wet seasons.

The total volume of water falling onto the Nata catchment was calculated as 6975, 18,450 and 9450 mcm for, respectively, the 1998-1999, 1999-2000 and 2000-2001 wet seasons. Annual river discharge via the Nata River was, therefore, 2.9, 2.9 and 0.7% of the annual precipitation totals in the Nata river catchment, excluding the north basin.

2.3.2.2 River input from the smaller rivers

Approximate calculations of the four remaining river catchment areas and the total volume of rainfall falling on each catchment, for each wet season, are presented (Table 2.4).

Table 2.4 Catchment areas and total volume of rainfall (10^6 m^3) estimated within each catchment, for each wet season.

River	Catchment Area (km^2)	1998-1999	1999-2000	2000-2001
Semowane	1050	430.5	882	336
Mosetse	1800	900	1476	594
Lepashe	800	369.6	696	224
Mosope	1750	770	1522.5	630

Predicted annual river discharge for each river, varies with each wet season (Figure 2.12). Of the four smaller rivers the Mosetse and Mosope rivers are the larger in terms of their contribution to the standing water on Sua Pan, each is substantially smaller than the Nata River. Discharge totals for each river, in order of wet season, were 12.5, 25.9 and 2.4 mcm for the Semowane, 26.2, 43.4 and 4.2 mcm for the Mosetse, 10.8, 20.5 and 1.6 mcm for the Lepashe, and 22.4, 44.8 and 4.5 mcm for the Mosope rivers.

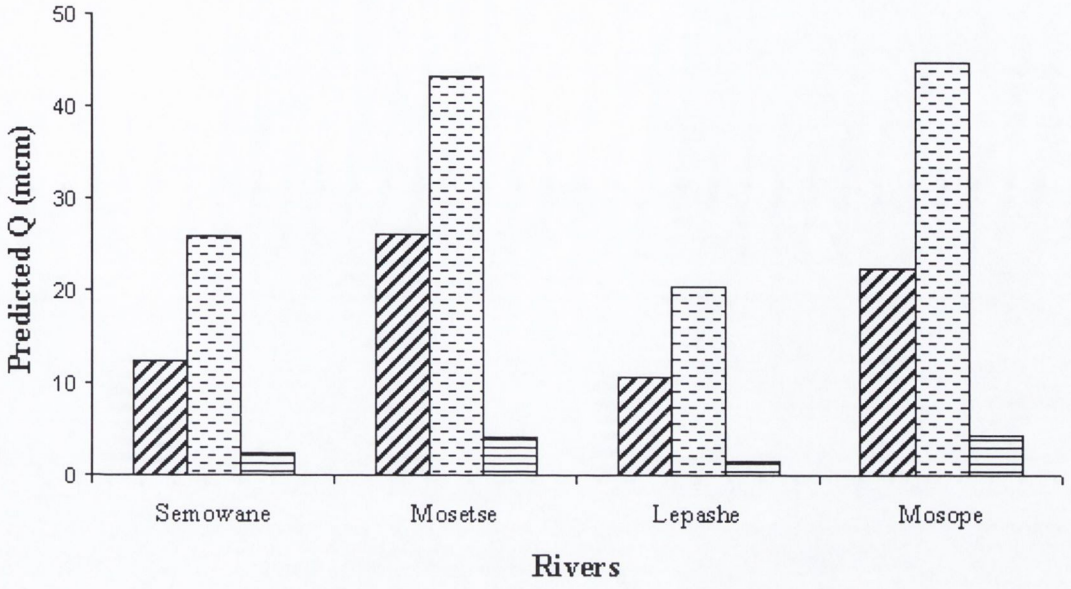


Figure 2.12 Annual river discharge onto Sua Pan by the Semowane, Mosetse, Lepashe and Mosope rivers during the 1998-99 ▨, 1999-2000 ▤ and 2000-2001 season ▤.

2.3.3 Direct input from precipitation

Surface areas calculated for the north, middle and south basins were, respectively, 975, 784 and 1903.5 km^2, giving a combined total area of 3662.5 km^2 for Sua pan. Total volume of water input from direct precipitation for the North, Middle and South basins, calculated as the net rainfall over the total area of each basin, was, respectively, 275, 221 and 526 mcm during the 1998-1999 wet season, 579, 465 and 1130 mcm during the 1999-2000 wet season and 158, 127 and 309 mcm during the 2000-2001 wet season. The figures for each basin are calculated from the same rainfall data collected at Sua pan Meteorological station.

2.3.4 Total flooding

2.3.4.1 Combined input

Assuming that the contribution of groundwater seepage is negligible, the lake basins on Sua pan floods to various extents during the wet season from the combined input of both the inflowing rivers and direct precipitation (Fig. 2.13). Total input into the north, middle and south basins were, respectively, 477, 247 and 559 mcm during the 1998-1999 wet season, 1121, 509 and 1195 mcm during the 1999-2000 wet season and 226, 132 and 315 mcm during the 2000-2001 wet season. Much of the temporary lake water comes from direct precipitation over the middle and south basins and only a small proportion comes from the inflowing rivers (Fig. 2.13). Discharge for the Nata River, however, contributed a considerable amount to the volume of water in the north basin.

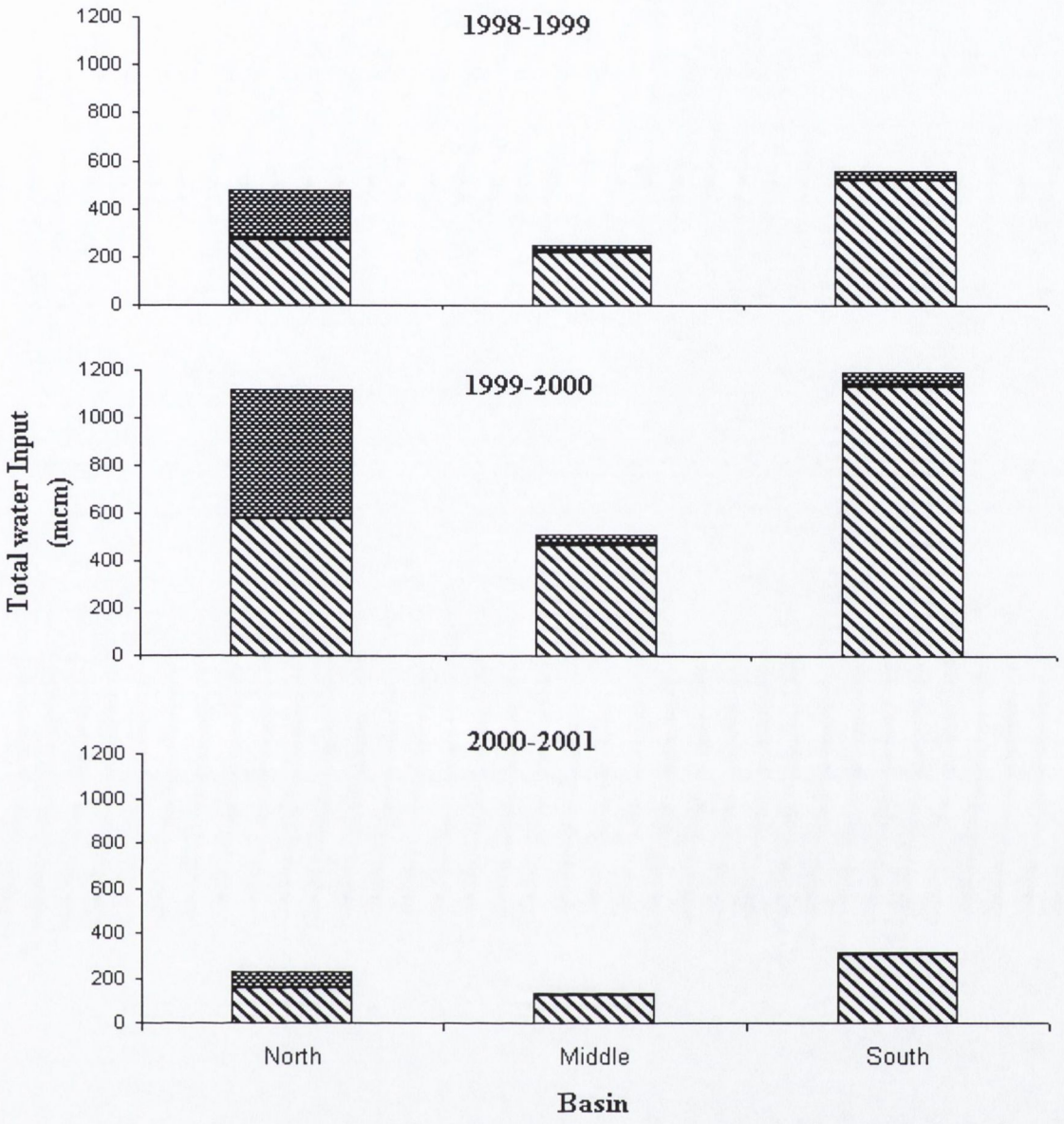


Figure 2.13 Total annual input of water into the three basins of Sua Pan, over three seasons, calculated from the combined input of river flow ▩ and direct precipitation ▨.

2.3.4.2 Period of the flooding

Mean annual evaporation rates, from October to September, for each year were calculated as 8.03, 7.3 and 7.73 mm d^{-1} for, respectively, the 1998-1999, 1999-2000, and 2000-2001 wet seasons. High daily evaporation rates contributed to a rapid disappearance of standing water in each basin, during each season and the predicted periods of flooding (calculated in days) are shorter than the time observed in the field (Table 2.5, Fig. 2.14).

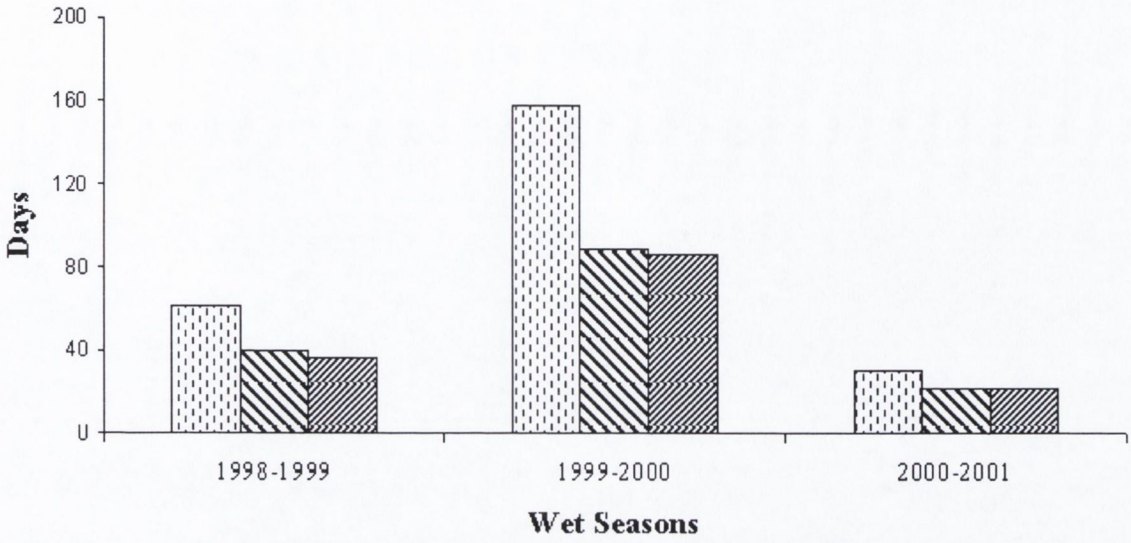


Figure 2.14 Predicted periods of flooding in the north, middle and south basins during the three wet seasons.

Table 2.5 Predicted period of flooding (in days) for each basin calculated from daily rainfall, river discharge and evaporation rates by the equation $(P + Q) / (E_d \times A) = L$. Observed flood periods are given in parenthesis.

Basin	1998-1999	1999-2000	2000-2001
North	61 (98)	157 (327)	30 (364)
Middle	39 (79)	89 (264)	22 (65)
South	37 (83)	86 (302)	21 (68)

Heavy showers resulted in brief periods of flooding at the beginning of the seasons and after substantial rainfall events each basin filled up and remained flooded for long periods (Table 2.5 and Fig. 2.15). The beginning and end of flooding varied owing to variations in local rainfall events, resulting in different spatial and temporal flood regimes among the basins.

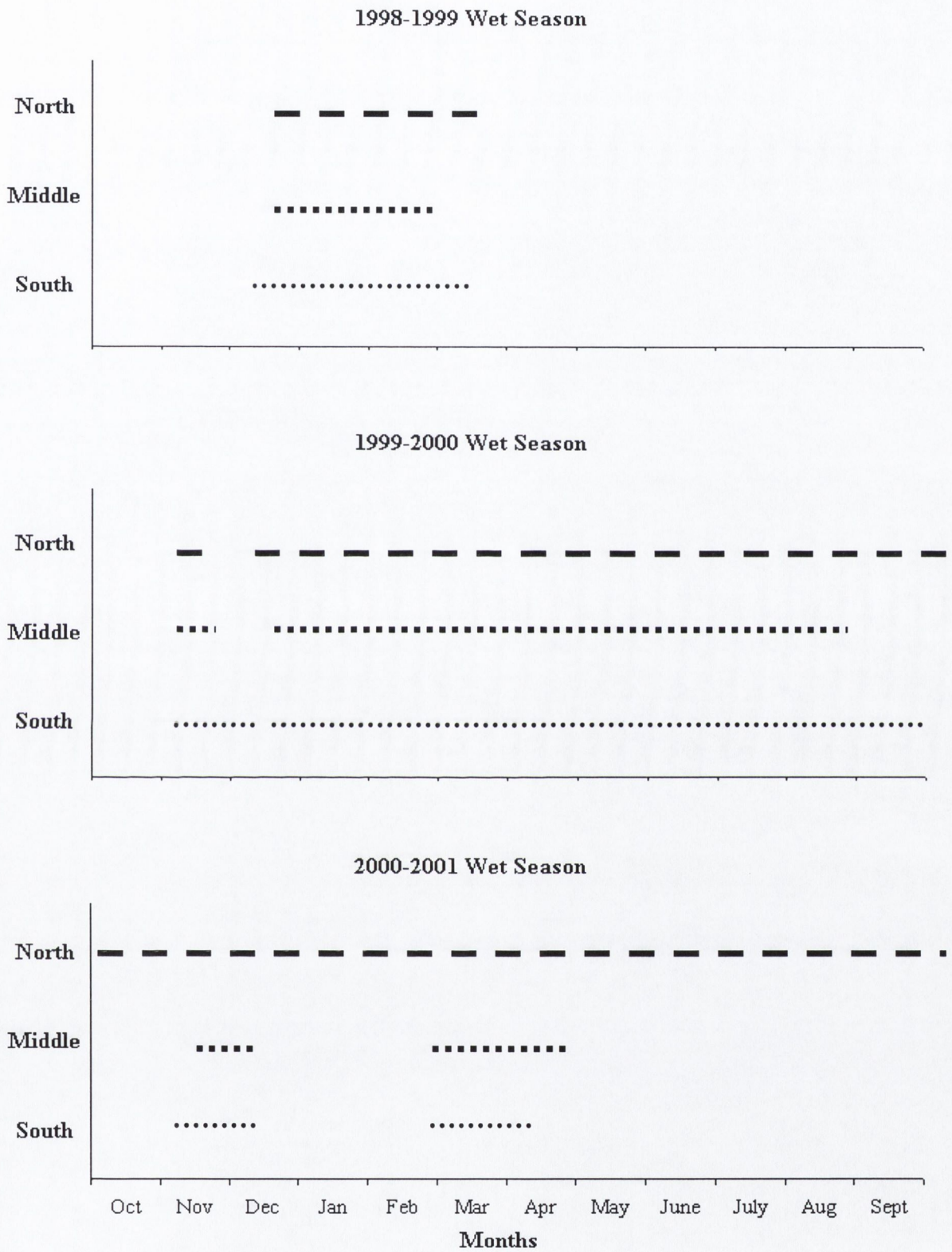


Figure 2.15 Duration of flooding periods in the north (▬ ▬), middle (▪▪▪▪) and south basin (·····) during the 1998-1999, 1999-2000 and 2000-2001 wet seasons. The lines represent periods of standing water in these three basins.

2.3.4.3 Area of the flooding

The area of flooding, calculated from TERRA satellite images, varied enormously between April 2000 and February 2001 (Fig. 2.16). Flood area increased from a small proportion of the north and south basin in December 1999 to floods that covered almost the entire pan in April 2000, before it gradually decreased to a recorded minimum in February 2001 (Table 2.6). The pan did not dry out completely until February 2002. From average lake depths among the basins, flood volume on Sua pan increased from an estimated 11.4 mcm in December 1999, to a recorded maximum of 1607.7 mcm in April 2000 (Table 2.6). After the rainfall stopped, the lake began to dry up and the volume decreased to an estimated 60.8 mcm by February 2001.

Table 2.6 Total area (*A*) and volume (*V*) of flooding on Sua pan, calculated from satellite images of Sua pan and average lake depths, on occasions during the 1999-2000 and 2000-2001 wet seasons. The area of some pans surrounding Sua pan is also given.

Date	Sua Pan A (km^2)	Small pans (km^2)	Mean depth (m)	V of Sua pan (mcm)
Dec 21st, 1999	190.5	0	0.06	11.4
April 18th, 2000	2593	724	0.62	1607.7
June 24th, 2000	1999.4	226	0.48	960
Aug 11th, 2000	1036.5	0	0.36	373.1
Feb 2nd, 2001	304	0	0.2	60.8

April 18th, 2000

June 24th, 2000

August 11th, 2000

February 2nd, 2001

Figure 2.16 Spatial and temporal patterns of standing water on Sua Pan, from April 18th, 2000 to February 2nd, 2001. Areas of flooding (▒) were measured from TERRA satellite images of Sua Pan (courtesy of the Jet Propulsion laboratory, NASA).

2.4. Discussion

Climate controls the amount of standing water on Sua pan through the processes of precipitation and evaporation. Over the three-year study period Sua pan experienced highly variable annual rainfall. This is consistent with the high variability in annual rainfall, reported for the area by Schulze (1972). As a result, flood duration varied considerably between the seasons (Fig 2.15). The 1998-1999 and 2000-2001 wet seasons were average and below average rainfall seasons according to Schulze (1972). Annual rainfall for the 1999-2000 wet season was, however, twice the mean annual amount for the area and one of the highest ever recorded. 2000 was an El Nino year, during which three tropical cyclones passed over southern Africa and gave rise to frequent, high intensity rainfall for days on end.

The temporal patterns of daily rainfall also had a large influence on the flooding regime of the pan during each wet season. Net rainfall results (Fig 2.7) indicate that only some rainfall events make a contribution to surplus water input. Average monthly temperatures, ranging from a maximum of 35 °C in the summer, to 25 °C in the winter (Fig. 2.5), were in agreement with ranges for the area described by Schulze (1972) and ensured high daily evaporation rates. Maximum rates were reduced somewhat during heavy rainfall months and inter-seasonal variation in evaporation was, therefore, far greater during the wet months of the year (Fig 2.6). Long intense rainfall events during the cyclonic storms of 1999-2000, for example, contributed to lower evaporation rates.

Catchment rainfall data indicated spatial and temporal variation in rainfall (Fig. 2.8). The spatial variation, expressed as the standard deviation (SD) of rainfall between the sites, was less pronounced during the 1999-2000 season (SD of 22.5mm) owing to the widespread nature of the seasons' cyclonic weather systems. Typical localised thunderstorms accounted for greater spatial variation (SD of 65.3 mm and 45.3 mm) during the other two seasons (Longley, 1976; Cooke, 1979*c*).

A strong relationship between Nata river discharge and depth (Fig. 2.10) suggests that depth records can be used to predict Nata river discharge. Such predictions, however, can lead to some significant degree of error at high levels of discharge. Discharge when the river was

2.5m in depth, for example, varied between approximately four and twelve million cubic meters. The amount and temporal patterns of river discharge is an important contributor to standing water on Sua pan. Nata River has a large catchment area with water retaining soils and vegetation cover that may have reduced the rainfall-runoff response at the beginning of the season (Fig 2.11). Contrary to typical semi-arid rainfall-runoff relationships (Yair & Lavee, 1985; Shaw, 1994), much of the initial rainfall that falls over the catchment is lost through evapo-transpiration or to the ground water reserves and only 0.7 to 2.9 % of the total volume falling on the catchment reached the pan. The lag period in runoff after rainfall events appears to decrease as the season progresses, suggesting that a water storage/retention threshold is reached. A large proportion of the Nata river discharge may, however, be dependant on higher rainfall in the upper parts of the catchment, on the Zimbabwean side (Thompson, 1965). The lack of rainfall data from the Zimbabwean part of the catchment could have, therefore, been a factor in the poor correlation between rainfall and runoff (Fig. 2.11). The existence of small dams on some of the river tributaries on the Zimbabwean side may have altered the rainfall-runoff regime even further.

River discharge figures predicted for the four smaller rivers were much lower than those for the Nata river (Fig. 2.13). These catchments are much smaller and hence the total yield was much less. Predicted discharge figures for the Mosetse river, of 26.2 mcm, 43.4 mcm and 4.2mcm during the three wet seasons (Fig. 2.12), were very close to the mean annual discharge figure of 26.4 mcm, calculated during an Environmental Impact Study on the Soda Ash Chemical Plant given by (Syratt & Martin, 1985). Smaller catchments, however, result in less evapo-transpiration loss owing to lower retention times (Yair & Lavee, 1985) and the ratio of rainfall volume to discharge was likely, therefore, to be considerably higher than that of the Nata river. Discharge from these rivers may be underestimates as a result. In general, river discharge as a proportion of the total water gain by each of the three basins varied and, apart from the Nata River, only accounted for a small amount of the total water gain. Direct precipitation appears to be a more important factor in terms of its contribution to the flooding of the basins (Fig. 2.15).

While river discharge underestimates may explain some of the large differences between predicted and observed flooding periods (Fig. 2.14, 2.15), ground water input, through sub-surface flow, was not accounted for and may play an important role in contributing to flood

volume and, consequently, to the period of flooding (Thomas, 1989). The suggestion that the Makgadikgadi is also a terminal sink for ground water from the middle Kalahari (Thomas & Shaw, 1991) certainly implies a large input of water as recharge from the ground water. The influence of ground water on the hydrological regime of Sua pan is, however, uncertain and further studies need to be carried out in order to quantify this water source. Loss to ground water may also occur in dry years. Studies carried by the Soda Ash Company (Botswana Ash (Pty) Ltd.) investigated the potential recharge of sub-surface brines from the surface waters using piezometers and tritium isotope concentration studies. Piezometer studies indicated that infiltration of surface water reaches the sub-surface brine interface, at approximately 2 m, within a few days of heavy rainfall and river discharge. This ground water reserve may soak up rainfall and account for the rapid disappearance of initial floods observed at the beginning of the rainy seasons. Tritium isotopes from nuclear fallout over the past 20 years were traced to between 2 and 4 m, suggesting that there is a limited depth of infiltration from the surface and once the layers above this height are saturated, water loss from the surface occurs through evaporation alone. The possibility of water seepage to lower levels, whereby it reaches the brine that is being pumped out by the soda ash plant, is still under investigation using isotope studies. This being the case, the implications are serious if one considers Sua pans delicately balanced hydrological regime.

Flood volume on Sua pan in April 2000 was an estimated 57% of the total water input during the 1999-2000 wet season (Fig. 2.12). It is likely that the flood volume was considerably larger in February and March of that year owing to larger flood areas, observed from the air. No satellite images were, however, available for those months and volume calculations could not be made. The volume of water lost between April 18th and June 24th, and June 24th and August 11th 2000 were, respectively, 648 and 587 mcm. Average daily loss of water from Sua during these two periods was, therefore, estimated to be 9.3 and 11.5 mcm d^{-1}, or 10.4 mcm overall for the combined four month period. If one considers the average area of flooding between these two periods to be, respectively, 2296 and 1518 km^2 and the average depth, 0.55 and 0.42 m, then the rate of water loss from the lakes on Sua pan approximates to 2.2 and 3.2 mm d^{-1}. This is considerably lower than the average daily evaporation rate for that season, of 7.3 mm d^{-1} (Fig. 2.5), used to calculate predicted flood periods, and might explain the large difference between predicted and calculated flood periods.

The existence of temporary water bodies varies considerably depending on the magnitude of and temporal relations between water income and water loss. The duration of flooding on the pan, in turn, has profound affects on other abiotic characteristics and on the biological components of the lake ecosystem. Variable flood duration places physical constraints on the ability of crustaceans, for example, to survive to the reproductive stage (Hartland-Rowe, 1972; Williams, D.D. 1987; Meintjes *et al.*, 1994). Salinity, nutrient concentrations and turbidity in temporary waters vary considerably with river discharge and water levels (Chapter 3) and, in turn, affect temperature and light regimes, which play a crucial role in primary and secondary productivity (Chapters 4 and 5). Finally, the temporal patterns of wet and dry phases control the food availability and breeding success of the migratory flamingo populations that congregate on Sua pan when it floods (Chapter 6).

Chapter 3

Water chemistry

3.1 Introduction

3.1.1 Salinity and pH

3.1.1.1 Salinity in temporary lakes

Salinity is best defined as the sum of all ionic constituents present in water and is considered one of the most important chemical attributes of inland saline lakes (Hutchinson, 1957; Williams & Sherwood, 1994; Williams, 1998). The acquisition of solutes occurs, principally, through (i) chemical weathering of the rocks in the drainage basin, (ii) organic matter and the products derived from biota in the basin, (iii) atmospheric precipitation and dry deposition (iv) exchanges of ions, both in the gaseous form, through the air-water interface, and as chemical solutes, through the water-sediment interface (Talling & Lemoalle, 1998). An important control on temporary lake salinity is hydrological regime, both in relation to climatic factors controlling water input and loss, and in the relative contributions of surface water and groundwater effects to chemical composition (Langbein, 1961; Shaw & Thomas, 1989). During dry periods evaporation draws ground water to the surface, which evaporates and results in the precipitation of efflorescence such as halite and trona (Eugster & Hardie, 1978; Shaw & Thomas, 1989). The amount of surface efflorescence is greatly influenced by the length of the dry periods between floods. Basins with large surface inflows are, therefore, unlikely to develop significant evaporite deposits and, in arid climates, lake salinity is influenced to a larger degree by groundwater and surface efflorescence (Hardie *et al.*, 1978; Shaw & Thomas, 1989). Seasonal flooding re-dissolves the most soluble evaporites like halite, sodium carbonates and sulphates and returns their constituents to the surface and interstitial waters, while some of the least soluble minerals, such as Ca^{2+} Mg^{2+} and SO_4^{2-} carbonates and Mg^{2+} and Na^{+} silicates, remain in crust or particulate form in the sediment (Eugster & Jones, 1977; Eugster & Hardie, 1978). Highly saline intermittent lakes, therefore, tend to be dominated by fewer ions of high concentrations.

3.1.1.2 Defining salinity

Since conductivity (or specific conductance), is a measure of the ease of electrical current flow in solutions, which increases as the number of ions increase, it reflects total ion concentration or salinity of a solution (Williams, 1966; Hammer, 1978*b*; Williams, 1986; Williams & Sherwood, 1994). Ionic composition varies both in absolute total salinity and in relative, equivalent percentages of the different ions. Na^+, for example, is the most common cation in most saline waters but varying combinations with the major anions, like Cl^-, $HCO_3^- + CO_3^{2-}$, and SO_4^{2-}, can occur. Salt lakes are, therefore, often typified chemically as sodium chloride (NaCl), chlorocarbonate ($NaCl > HCO_3^- + CO_3^{2-}$), chlorosulphate ($NaCl > SO_4$), carbonate ($NaHCO_3 + CO_3^{2-}$), or carbonate-chloride ($NaHCO_3 + CO_3^{2-} > Cl^-$) lakes, according to predominant anion compositions (Eugster & Hardie, 1978; Williams, 1998). Relative ionic proportions in saline lakes are often displayed in the form of ternary diagrams, which enable visual recognition of different ionic compositions (e.g. Eugster & Hardie, 1978; Seaman *et al.*, 1991; Day, 1993; Williams, 1998).

3.1.1.3 Regional characteristics in Africa

Geographical variation in the salinity of saline lakes occurs owing to different origins of the dominant ions (Eugster & Hardie, 1978; Shaw & Thomas, 1989; Williams, 1998). Weathering of limestone-rich rocks, for example, results in high concentrations of HCO_3^- and CO_3^{2-} ions, while volcanic lavas can contribute to large inputs of silicate. Na^+ and Cl^- are, however, dominant ions in most saline lakes of the world (Hammer, 1986; Kilham, 1990; Comin & Williams, 1994). This is generally true for salt lakes in Africa, although HCO_3^- and CO_3^{2-} are dominant anions in the soda lakes of East Africa and ionic composition can differ considerably among regions and between lakes in close proximity to each other (Talling & Talling, 1965; Ashton & Schoeman, 1983; Livingstone & Melack, 1984; Day, 1993). Although conditions vary in East Africa, the general composition of closed basin lakes consists of high concentrations of Na^+ and $HCO_3^- + CO_3^{2-}$ ions, with accompanying high pH of 10 or more (Talling & Talling, 1965; Melack & Kilham, 1972; Hecky & Kilham, 1973; Wood & Talling, 1988). In the relative absence of Ca^{2+}, $HCO_3^- + CO_3^{2-}$ do not readily precipitate out and, therefore, increase steadily

with total salinity. In southern African saline lakes, where Cl^- is the dominant anion (Seaman *et al.*, 1991; Day, 1993), ionic compositions are quite different to those in East Africa. In general, despite the diverse geochemistry of their substrata, the saline lakes in South Africa and Namibia are sodium chloride and sodium chloro-carbonate lakes, dominated by Na^+ and Cl^- ions, while $HCO_3^- + CO_3^{2-}$ are abundant in lower salinity waters (Hutchinson *et al.*, 1932; de Bruiyn, 1972; Ashton & Schoeman, 1983; Seaman *et al.*, 1991; Silberbauer & King, 1991; Day, 1993).

3.1.1.4 Background to the salinity of the Makgadikgadi

The chemical composition of lake Makgadikgadi is poorly understood and is not considered in the literature reviewing saline water chemistry in southern Africa (Mepham, 1987; Seaman *et al.*, 1991; Day, 1993). Similarly, the chemistry of numerous temporary saline pans that exist in the southern Kalahari region of Botswana is absent (Lancaster, 1974; 1978). In South Africa, the chemical composition of similar lakes comprises, predominantly, salts of geological origin ($Na^+ > Ca^{2+}$ and Mg^{2+} chloride and sulphate rich rocks), although 'cyclic salts' have also been proposed as important contributions (Hugo, 1974; Seaman *et al.*, 1991; Day, 1993). Stansfield (1973) suggests that solutes in Sua pans inflowing rivers contribute to the chemical composition in its basins, although little information on the chemical composition of these rivers exist. Seaman *et al.* (1991) argue that Makgadikgadis water chemistry might vary from the common regional ionic composition of southern African waters owing to the fact that its crustacean species and community diversity is more analogous to that of East African salt lakes.

The surface of Sua pan consists of brine-saturated sand and clay layers with surface efflorescence of trona (Na_2CO_3-Na_2HCO_3-$2H_2O$) and halite (NaCl) (Ebert & Hitchcock, 1978; Thomas & Shaw, 1991). Large amounts of sodium chloride, carbonates and sulphates exist on and in the top layers of the pan surface (Shaw *et al.*, 1988). These salts are derived from the chemical weathering in the surrounding catchment, where $CaCO_3^-$ rich rocks and soils are an important influence (Thomas & Shaw, 1991). Efflorescence crusts occur in areas of dry pan where the presence of highly saline goundwater exists

close to the surface. Evaporative 'pumping' draws this groundwater to the surface and precipitation of these highly soluble minerals occurs (Eugster & Hardie, 1978). Where efflorescence occurs, the acquisition of a heavy solute load after flooding influences the salinity and chemical composition of standing waters.

3.1.1.5 Seasonal fluctuations and changing ionic proportions

Salinity can also vary enormously over individual flood periods owing to highly variable hydrological regimes (Hartland-Rowe, 1972; Seaman & Kok, 1987; Shaw & Thomas, 1989; Meintjes *et al.*, 1994; Allan *et al.*, 1995). The temporal patterns of change in the salinity over a season are, therefore, dependant on changes in the dissolution and evaporative concentration processes and can be closely correlated with depth changes in a lake (Williams, 1991; Hardie *et al.*, 1978; Shaw & Thomas, 1989). A series of geochemical pathways with increased evaporative concentration gives rise to the progressive precipitation of salts, which accumulate on and in the sub-surface layers of the sediment to form mineral precipitates as the lake dries up (Stumm & Morgan, 1970; Hardie *et al.*, 1978). The evolution of evaporates is determined by the ratios of solutes present and their precipitation gradient. The sequential precipitation of different salt combinations in waters, with ionic compositions close to that of sea water, begins with $CaCO_3$, followed by $CaSO_4$ at salinities of between 40-100 g l^{-1}, NaCl at approximately 200-350 g l^{-1}, and then the less common salts like KCl and $MgCl_2$ (Sonnenfeld, 1984; Hardie *et al.*, 1978; Eugster & Hardie, 1978). In South Africa, temporary pans show increasing loss of Ca^{2+} and HCO_3^- ions by precipitation with an increase in salinity and the proportion of Na^+ and Cl^- ions increases as a result (Seaman *et al.*, 1991; Day, 1993). Apart from work carried out by Moss & Moss (1969), Ashton & Schoeman (1983), and Meintjes *et al.* (1994), few comprehensive long-term studies examined salinity changes in saline lakes within southern Africa (Seaman *et al.*, 1991; Day, 1993).

3.1.1.6 pH values in southern Africa

Values for pH in African saline lakes are generally high, ranging between 8 and 11 (Hutchinson *et al.*, 1932; Talling & Talling, 1965; Melack, 1978; Allan *et al.*, 1995). Values increase with increasing conductivity, although the reverse can happen in very

high saline conditions (Stumm & Morgan, 1970; Williams, 1998). pH is a measure of the hydrogen ion concentration, which, in turn, is controlled by the inorganic carbon equilibrium, $CO_2 - H_2CO_3 - HCO_3^- + H^+ - CO_3^{2-} + 2H^+$, which fluctuates diurnally according both chemical and biological activities (Stumm & Morgan, 1970). Changes result from the alternating input and removal of CO_2, which alters the relative concentrations of carbonic acid ($H_2CO_3^-$) and H^+ ions. Sources of CO_2-carbonic acid, in solution, include the atmosphere, rainfall and/or river inflow and biological respiration, while the removal/uptake of CO_2 from solution occurs through photosynthesis and mineral dissolution processes (Stumm & Morgan, 1970; Horne & Goldman, 1994). Changes in pH associated with photosynthesis and CO_2 uptake can be dramatic and can occur within hours of increased photosynthetic activity. Some very eutrophic lakes and some soda lakes have pH values as high as 10 to 11.5 (Hutchinson *et al.*, 1932; Talling & Talling, 1965). At such high concentrations, ammonium can become toxic to the biota and limit species richness and abundance (Horne & Goldman, 1994). CO_2 uptake, to concentrations of equilibrium with atmospheric carbon dioxide pressure, can increase under wind induced turbulent conditions, although high concentrations of bicarbonate and carbonate ions in some salt lakes act as important buffers and prevent any major pH shift as a result of increased CO_2 uptake (Stumm & Morgan, 1970).

Little is known about the pH of southern African saline waters but data collected from various lakes around South Africa have typical ranges of 7-9 (Hutchinson *et al.*, 1932; Seaman & Kok, 1987; Day & Seely, 1988; Mepham, 1987; Meintjes, *et al.*, 1994). Maximum values were recorded on those pans where HCO_3^--CO_3^{2-} are important anions, for example, at Etosha (9.2) and Pretoria Salt Pan (10.4) (Berry, 1972; Ashton & Schoeman, 1983). pH values taken from small pans adjacent to Sua pan, by the Rhodesian Schools Exploration Society in 1957, were 9 and 10 (Eccles, Undated). The report from this expedition suggests that pH is one of the most important factors controlling the occurrence of high pH tolerant algae and crustacean species on the Makgadikgadi pans.

3.1.2 Nutrients

3.1.2.1 Nutrient loading and regeneration in African saline waters

Nutrient loading in lakes comes from river inflow, rainfall, and animal and bird faeces (Horne & Viner, 1971; Viner & Smith, 1973; Burgis *et al.*, 1973; Ganf & Viner, 1973). After seasonal rains, the flooding of surrounding oxidised/aerated soils, decomposed flora, and animal dung causes the rapid release of large amounts of nutrients into inflowing river water (McLachlan, 1971; Howard-Williams, 1972; Gaudet & Muthuri, 1981). Nitrate (NO_3^--N) is released quickly from soils, being the most soluble form of nitrogen under aerobic conditions (Horne & Goldman, 1994). Studies done in East Africa have estimated inputs of nitrogen (mainly in the form of nitrate) by rainfall to be very high, with maximum annual inputs of 1-4 g m^{-2} y^{-1} (Visser, 1961; 1964; Thornton, 1965; Viner, 1973). Phosphorus comes in the form of organic and inorganic phosphorus in an available soluble form or as particulate phosphorus bound to particles (Horne & Goldman, 1994). Small amounts of phosphorus can enter lakes from rainfall originating from wind-blown dust. Other inputs included in inflow waters are small amounts of inorganic phosphates originating from the weathering of rocks (Horne & Goldman, 1994). Nutrient regeneration from lake sediment is also an important source of nutrients in temporary saline lakes and is influenced enormously by lake morphology (Lennox, 1984; De Groot, 1981; Marsden, 1989). Nutrient adsorption and release from the sediment is controlled by redox potentials (MacIntyre, 1975; Peters & MacIntyre, 1976; Bostrom & Petterson, 1982; Bostrom *et al.*, 1988). Windy conditions increase turbidity (mixing of sediment into suspension) and oxic conditions at the sediment-water interface and has, therefore, a major influence on nutrient regeneration from the sediment (De Groot, 1981; Lennox, 1984; Livingstone & Melack, 1984). Orthophosphate release from sediment particulate matter, in the form Fe^{3+} and Al^{3+} complexes, occurs when these complexes are reduced under anoxic (low redox) conditions and become soluble. Ammonium, produced by the bacterial decomposition of organic detritus, is quickly oxidised to nitrate in the oxygenated upper layers of the sediment, which slowly diffuses into the lake water above. Under anoxic conditions, however, available nitrate can be lost by its conversion to nitrogen gas, through denitrification. When nitrogen is limiting,

nitrogen fixation by blue-green algae and bacteria converts nitrogen gas (N_2) from the atmosphere into ammonium, in specialised, anoxic cells called heterocysts, increasing nitrogen input from the atmosphere substantially where blue-green algae occur in abundance (Horne & Goldman, 1994).

The inputs and recycling of nutrients by animals and birds contribute significantly to nutrient loading and regeneration in African salt lakes (Horne & Viner, 1971; Ganf & Horne, 1975). Where populations are large relative to the volume of water in the lake, nutrient input from the droppings of birds can be quite considerable (e.g. Scherer *et al.*, 1995; Hoyer & Canfield, 1994; Manny *et al.*, 1994). Marion *et al.* (1994) estimated that droppings from large birds contributed up to 36 % of annual nitrogen input and 95% of annual phosphorus input, in Grand-Lieu Lake, France. This form of nutrient loading and regeneration may be particularly important in some shallow African soda lakes, where dense flamingo populations number hundreds of thousands (Jenkin, 1957; Brown, 1975; Brown *et al.*, 1982; Berry, 1972). The action of flamingo footsteps and feeding behaviour also enhances nutrient release by stirring up sediment into suspension (Comin *et al.*, 1997). Vareschi (1978) has estimated that the flamingos of Lake Nakuru, Kenya consume as much as 93 % of daily primary production, suggesting a very rapid and almost complete diel regeneration of lake nutrients. The regeneration of nutrients by zooplankton excretion and the excretion of dissolved organics by phytoplankton has been suggested as another important factor in the regenerative processes among African lakes (Ganf & Viner, 1973; Livingstone & Melack, 1984).

Nitrate is frequently a limiting factor for algal growth in some African waters (Prowse & Talling, 1958; Talling & Rzoska, 1967; Moss, 1969) and nitrate loss, attributed to low O_2 concentrations and high pH, have been reported in a variety of African saline lakes (Talling & Talling, 1965). The concentration of phosphorus, on the other hand, is often high in many saline lakes (Talling & Talling, 1965; Hartland-Rowe, 1972; Melack, 1978; Ashton & Schoeman, 1983). High photosynthetic rates observed in some lakes in Africa have been attributed to rapid internal recycling that keep nutrient supplies in excess of demand, even though some nutrients occur at limiting concentrations (Talling *et al.*, 1973; Melack & Kilham, 1974).

3.2 Materials and methods

3.2.1 Salinity and pH

3.2.1.1 Conductivity and pH

Conductivity and pH measurements commenced in December 1999, at the onset of flooding. Water samples were taken from sites in the north, middle and south basins of Sua Pan (Fig 3.1) on a bi-weekly basis, from December 1999 to July 2000, and on a weekly basis, from November 2000 to July 2001. Sampling dates for each basin differed slightly on occasion owing to differences in their temporal flooding patterns. During the 1999-2000 wet season samples from the south basin were less frequent owing to the inaccessibility of the area during periods of high rainfall. Plastic sampling bottles were rinsed three times with distilled water prior to sampling. Conductivity and pH samples were measured on the same day using a Mettler Toledo® MC 266 Conductivity Meter. Conductivity readings were corrected to 25^0C. The pH meter was calibrated using buffers of pH 7 and 9 before each pH measurement. Sampling ended in June 2000 while all three basins were still partially flooded. The middle basin dried out in August 2000 and the south in September. In November 2000, the north basin was still flooded when sampling resumed at the onset of the 2000-2001 wet season. Sampling of the middle and south basins during the 2000-2001 wet season covered the entire period from initial flooding to their drying out. The north basin, however, remained flooded after June 2001 and a substantial body of water remained when sampling stopped.

3.2.1.2 Total ionic composition

Total ionic composition and the proportions of the most abundant ions, in water of Sua Pan and some of its rivers, were determined for the wet season of 1999-2000. Samples were collected in 500 ml plastic bottles, previously washed with a 5% acid solution and then rinsed three times with distilled water, from designated sites in the three basins and in three of the inflowing rivers (Fig. 3.1, Table, 3.1 & 3.2). Samples were stored at 4^0C until analyses was carried out by research hydrologists at the National Centre for US

Geological Survey (12201 Sunrise Valley Drive, Reston, VA 20192). Metals were analysed by atomic absorption spectrophotometry, chloride and bicarbonate were measured titrimetrically and sulphate gravimetrically. The major ions measured were Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, HCO_3^{-}, SO_4^{2-}, NO_3^{-}, Si^{-}, Sr and Br. Relative percentages of the major anions and cations, (Na^{+}, K^{+}, Ca^{2+}, Mg^{2+}, Si^{-}, Cl^{-}, HCO_3^{-}, and SO_4^{2-}), were calculated and illustrated on ternary diagrams in order to visualize the dominant ions and classify the waters according to Eugster & Hardie (1978) and Williams (1998). Changes in ionic proportions with evaporation were illustrated by plotting the dominant cationic and anionic ratios against total dissolved solids (TDS). The ratio of Na^{+} : $Na^{+} + Ca^{2+}$ and Cl^{-} : $Cl^{-} + HCO_3^{-}$ were plotted against the TDS values to show changes in the composition of the major cations and anions with changes in salinity.

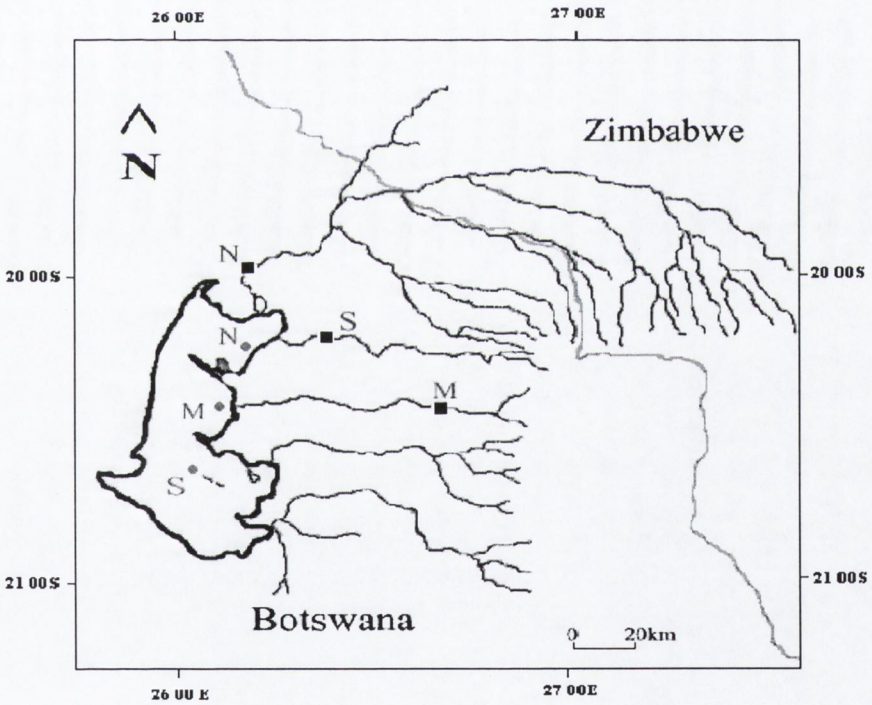


Figure 3.1 Map of the sampling positions on and around Sua Pan. The black squares mark the sites where ion composition samples were taken from the Nata (N), Semowane (S) and Mosetse (M) rivers. The grey circles mark locations where, conductivity, ion composition, pH, TP and TN samples were taken from the north (N), middle (M) and south (S) basins.

Table 3.1 Sample dates and locality (GPS co-ordinates in degrees and minutes) of water sampling from the Nata, Semowane and Mosetse rivers.

Samples	Nata River ($20^0$12'S $26^0$11'E)	Semowane ($20^0$25'S $26^0$23'E)	Mosetse ($20^0$38'S $26^0$39'E)
1	27th Nov, 1999	27th Nov, 1999	27th Nov, 1999
2	9th Jan, 2000	9th Jan, 2000	8th Jan, 2000
3	4th Feb, 2000	-	5th Feb, 2000

Table 3.2 Sample dates and locality (GPS co-ordinates in degrees and minutes) of water sampling from the basins of Sua Pan.

Samples	North ($20^0$20'S $26^0$15'E)	Middle ($20^0$36'S $26^0$07'E)	South ($20^0$48'S $26^0$02'E)
1	16th Dec, 1999	12th Dec, 1999	17th Dec, 1999
2	13th Jan, 2000	13th Jan, 2000	-
3	4th Feb, 2000	5th Feb, 2000	-
4	7th Mar, 2000	8th Mar, 2000	9th Mar, 2000
5	-	10th Apr, 2000	14th Apr, 2000

3.2.2 Nutrient analyses

Water samples were collected for analyses of total nitrogen (TN), total phosphorus (TP) and total dissolved phosphorus (TDP). Bi-weekly nutrient sampling was carried out during the 2000-2001 wet season in all three basins (Fig 3.1). Dates of sampling and sampling frequency changed slightly between the basins owing to different flooding regimes (Table 3.3). Samples were taken from the top 15-20 cm of the water column (in waters deeper than 20 cm) and collected in 50 ml glass bottles with Pyrex lids, previously acid washed and rinsed with distilled water. Two replicate samples were taken for TP and TDP, making a total of four samples on each sampling occasion, at each site. Water that was later used for TN analyses was taken from the TP bottles (25 ml for TP and 25 ml for TN). On the day the samples were taken, the TDP samples were filtered using Whatman GFC filter paper (previously rinsed with distilled water), using a vacuum pump and flask. The samples were returned to their freshly rinsed bottles and placed in storage at 4^0C.

Table 3.3 Date and locality (GPS co-ordinates in degrees and minutes) of nutrient sampling in the basins of Sua Pan, Makgadikgadi, with total phosphorus and total nitrogen samples taken on occasions indicated by **X**, and total dissolved phosphorus sampled on occasions marked with **Y**. The presence of standing water in each basin is indicated by a bold point (•).

Date	North ($20^0$12'S $26^0$11'E)	Middle ($20^0$25'S $26^0$23'E)	South ($20^0$38'S $26^0$39'E)
23rd Nov, 2000	• **X**		
29th Nov, 2000	•	• **X**	
22nd Dec, 2000	• **X**		
11th Jan, 2001	• **X, Y**		
27th Jan, 2001	• **X, Y**		
11th Feb, 2001	• **X, Y**		
25st Feb, 2001	• **X, Y**		
28th Feb, 2001	•	• **X, Y**	
8th Mar, 2001	•	•	• **X, Y**
13th Mar, 2001	•	• **X, Y**	•
27th Mar, 2001	• **X, Y**	• **X, Y**	• **X, Y**
1st June, 2001	• **X, Y**		

In July of 2001 all sample bottles were brought back to Dublin for analyses of TP, TDP and TN concentrations in the laboratory.

a) Total Phosphorus (TP)

The procedure used for phosphorus analyses followed the standard procedure methods used by Eisenreich *et al.* (1975). From each TP bottle and from a set of phosphate standard dilutions, 25 ml was placed in glass bottles, to which 5 mls of acid persulphate was added. Bottles were placed in an autoclave at 120^0C and 15 psi, for 30 minutes. Digestion converted organically bound phosphorus to measurable phosphate. The samples were left to cool and settle over night. Each sample was then transferred to test

tubes and diluted by a dilution factor of 5 using a Cavro® dilution machine. Molybdate mixed reagent was then added at a ratio of 1:5 and after 10 minutes absorbance at 822 nm was measured using a spectrophotometer. A standard curve was constructed using the standards and the mean absorbance (from two samples) for each site was then used to calculate the amount of phosphate present in each sample.

b). Total Dissolved Phosphorus (TDP)

The same procedure was carried out on 25mls of sample from each of the filtered TDP samples and phosphate was measured at 822nm and calculated using the same standard curve.

c). Total Nitrogen (TN)

The process used to determine TN was the same as the process used for TN analyses of seawater by Grasshoff *et al.* (1999). The oxidizing reagent used was a solution of 1.5 g NaOH, 5 g of $K_2S_2O_8$ (low in nitrogen) and 3 g of Boric acid made up to 100 ml in distilled water. Standard Nitrogen concentrations were made up to 25 ml (in the range of 0.2-4.0 mg l^{-1}). Oxidizing reagent was added to the standards and samples at a ratio of 1:10, and the bottles were placed in the autoclave at 15 psi for 30 minutes. Digested solutions were transferred to 3.5 ml cups and 70 µl of ammonium chloride buffer was added (1:50 concentration). Nitrogen was converted to nitrite by reduction on a cadmium column, and measured colourimetrically at 540 nm, using a Tecator® Flow Injection Analyses (FIA) machine.

d). Nitrate (NO_3^--N)

Nitrate (NO_3^--N) analyses of the river discharge waters from the Nata, Mosetse and Semowane, was carried out by the US Geological Survey laboratory in conjunction with analyses of total ionic composition, using standard analytical methods. The samples were stored at 4°C, shipped to the United States and analysed in July 2000. Samples were analysed, therefore, after a period of up to six months (depending on the dates the samples were taken). NO_3^--N may have been transformed and its quantity altered during this storage period and this was taken into consideration when interpreting the results.

Concentrations of nitrogen to phosphorus in mmol l^{-1} were calculated, using the atomic weights of, respectively, 14 and 31, in order to estimate the atomic N:P ratios for each sampling date in each basin.

3.2.3 Statistical methods

The differences in salinity among the three basins of Sua Pan and its change in each over time was tested using Repeated Measures ANOVA (RM-ANOVA) on Data Desk® Version 6. RM-ANOVA is an extension of the paired *t*-test, allowing for the analyses of the effects of many factors over time (or space). Three factors were considered; salinity being the dependent variable and basin and sampling date the two independent variables, with sampling date providing repeated measures on basins. Sampling date was treated as random and was nested within basins. Only results from samples taken at all three basins on the same dates were used in the test. There were, however, data missing from the south basin for some of the sampling dates. Salinity (conductivity) values were square root transformed in order to normalize the data before carrying out the test, with data normality investigated using normal-probability plots. A similar RM-ANOVA test was carried out, with H^+ concentration as the dependent variable, to test the variation in pH among the three basins during the 1999-2000 and 2000-2001 wet seasons. H^+ values were also square root transformed for normality.

The Pearson Product-Moment correlation was used to test hypothesis of linear association between two parametric variables, using Data Desk® Version 6. This correlation was used to test associations between conductivity and the variables pH, total dissolved solids, total phosphorus and total dissolved phosphorus as a proportion of total phosphorus. All variables were normalised by square root transformation.

3.3 Results

3.3.1 Conductivity

Conductivity results (in μs cm^{-1} at 25^0C), for the north, middle and south basins, during the 1999-2000 and 2000-2001 wet seasons, showed significant spatial differences (RM-ANOVA, $F_{1,54} = 265$, $P \leq 0.0001$; dependent variable was square-root transformed) (Figs 3.2 and 3.3). The north basin was the least saline ranging from 320 to 1780 μs cm^{-1} in 1999-2000 and 12,400 to 24,400 μs cm^{-1} in 2000-2001. Scheffe Post Hoc tests showed the north basin was significantly less saline than the middle basin ($P = 0.002$) and the south basin ($P \leq 0.0001$). The middle basin salinity increased from 730 to 91,600 μs cm^{-1} in 1999-2000 and from 2800 to 65600 μs cm^{-1} in 2000-2001 and it was significantly more saline than the south ($P = 0.0002$). The most saline conditions and the largest differences in conductivity from the beginning to the end of both flooding seasons were found in the south basin. Here conductivity increased from 22,400 to 111,000 μs cm^{-1} in 1999-2000 and from 46,800 to 125,800 μs cm^{-1} in 2000-2001. Conductivity results in the middle and south basins, at the beginning of each wet season, varied depending on the amount of initial flooding.

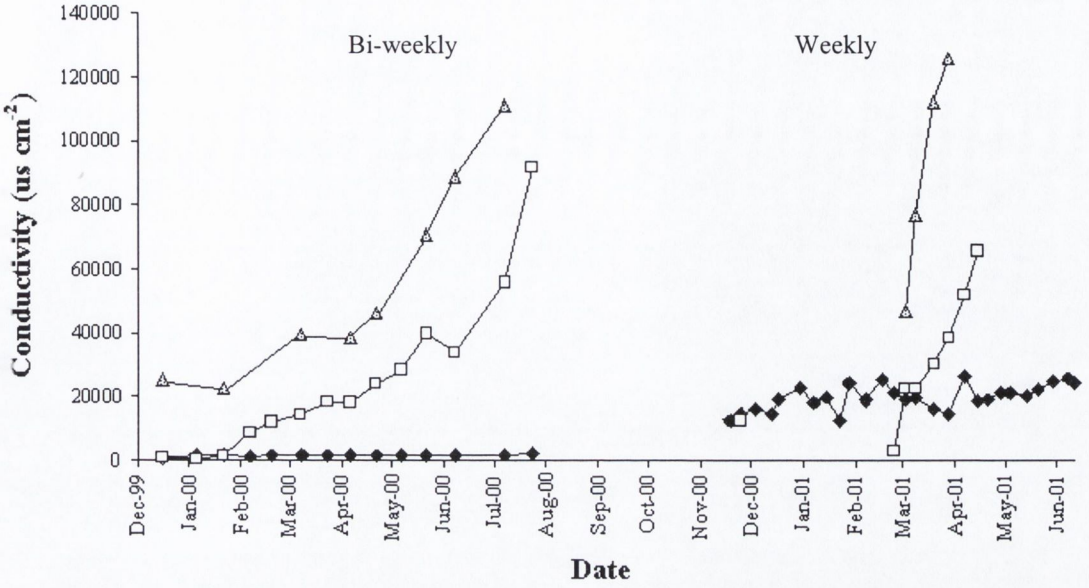


Figure 3.2 Conductivity results from the north ◆ , middle □ and south basin △, during the 1999-2000 and 2000-2001 wet seasons, with frequency of measurements indicated.

3.3.2 pH

The pH results for the north, middle and south basins were high and fluctuated frequently (Fig. 3.3). A significant difference in the pH results from the three basins, however, was observed (RM-ANOVA, $F_{1,53} = 593$, $P \leq 0.0001$; dependant variable was square-root transformed). Scheffe Post Hoc testing showed that values for the north basin were significantly lower than the middle basin ($P = 0.006$) and south basin ($P = 0.0002$). Results from the middle and south basins showed no significant difference ($P = 0.263$). The highest value (pH of 10.1) was measured in the north basin at the beginning of the flood. Values then decreased and fluctuated between 8.56 and 9.44 for the duration of the 1999-2000 season. Results gradually increased in the same floodwater, from 9.06 to 9.76, during 2000-2001. pH in the middle basin was slightly higher than the north basin and fluctuated between 9.06 and 9.78 during the 1999-2000. During the 2000-2001 season, however, values showed a decline from 9.98 to 9.64 as the salinity increased. The highest values occurred at the beginning of both flood events during that season. In the south basin, pH results ranged between 9.15 and 9.89, during the 1999-2000 season, with a general decrease in values with increasing salinity. Similarly, a decline from 10.04 to

9.64 was observed during the 2000-2001 season. Again, the highest values for both seasons occurred at the beginning of the season. A weak positive relationship was observed between pH (H^+ ions) and conductivity, over the two seasons ($r = 0.47$, n = 74, $P \leq 0.001$; variables square-root transformed) (Fig. 3.4). Apart from the first result in December 1999, the pH values for the north basin showed a general increase as conductivity increased during the flood period. The relationship in the middle basin at low conductivities was similar, apart from the high values at the beginning of the flood periods during the 2000-2001 wet season. No increase in pH with conductivity took place in the south basin and values remained between 9.3 and 10. Again, the high values at the beginning of both seasons did not conform to the general correlation with conductivity.

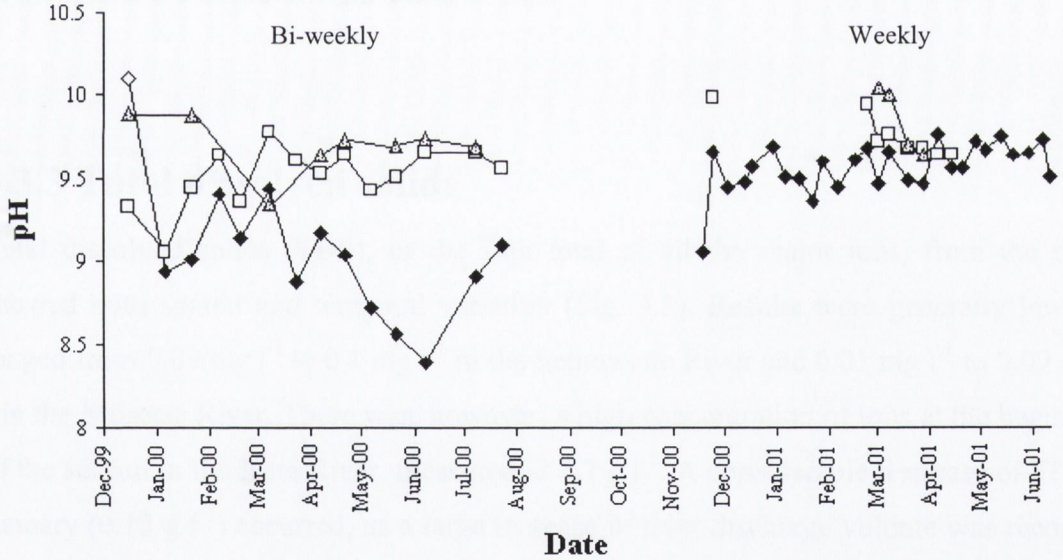


Figure 3.3 pH results as from the north ◆, middle □ and south basin △ during the 1999-2000 and 2000-2001 wet seasons, with the frequency of measurements indicated. Where results are missing, dotted lines represent periods of flooding between sample results.

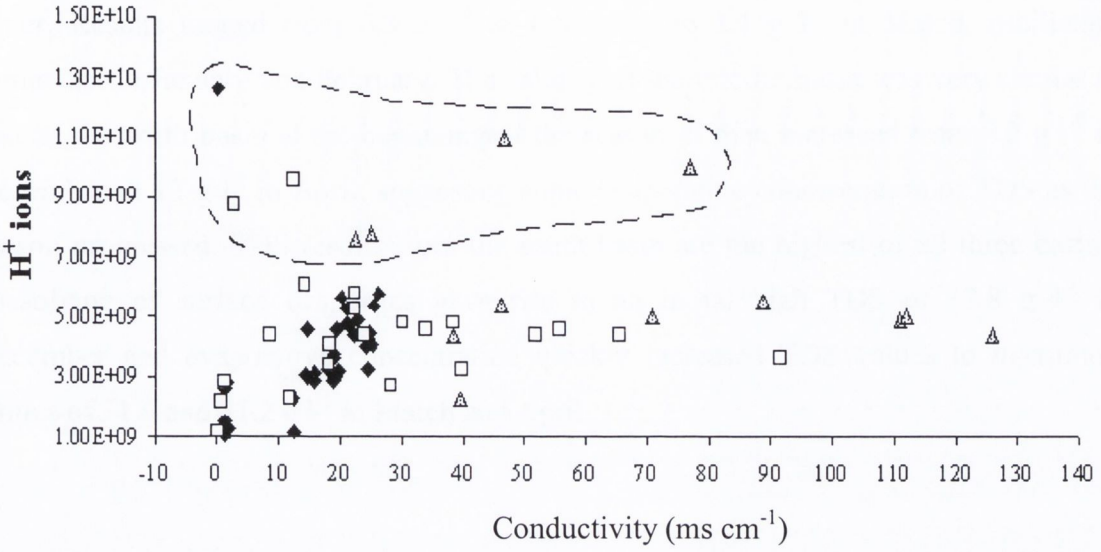


Figure 3.4 Relationship between H^+ ion concentration (pH) and conductivity in the north ◆ middle □ and south △ basin of Sua pan. Maximal values taken at the beginning of the floods are encircled with a dashed line.

3.3.3 Total dissolved solids

Total dissolved solids (TDS), or the sum total of all the major ions, from the rivers showed both spatial and temporal variation (Fig. 3.5). Results were generally low and ranged from 0.09 mg l^{-1} to 0.1 mg l^{-1} in the Semowane River and 0.01 mg l^{-1} to 0.09 mg l^{-1} in the Mosetse River. There was, however, a high concentration of ions at the beginning of the season in the Nata River, measured at 1.7 g l^{-1}. A considerable decrease of TDS in January (0.13 g l^{-1}) occurred, as a large increase in river discharge volume was recorded, before it increased again in February (0.24 g l^{-1}). Salinity in the Semowane and Mosetse rivers was lower and less variable. The Mosetse River did, however, show a progressive dilution of ions as the period of discharge increased. TDS ranged from 0.1 g l^{-1} in November to 0.09 mg l^{-1} in January to 0.01 g l^{-1} in February.

During the coarse of the season, TDS values increased along a north to south gradient (Fig 3.6). The salinity of the north basin was the lowest and varied the least throughout

the season owing to the large amounts of river discharge entering the basin from the Nata River. Results ranged from 0.3 g l^{-1} in December to 1.1 g l^{-1} in March, oscillating somewhat in January and February. The salinity of the middle basin was very similar to that of the north basin at the beginning of the season. It then increased from 0.2 g l^{-1} in December to 13 g l^{-1} in April, suggesting some evaporative concentration of TDS as the season progressed. TDS results from the south basin are the highest of all three basins. Dissolving of surface evaporites gave rise to an initial high TDS of 17.8 g l^{-1} in December and evaporative concentration quickly increased TDS values to maximum values of 31.6 and 31.2 g l^{-1} in March and April.

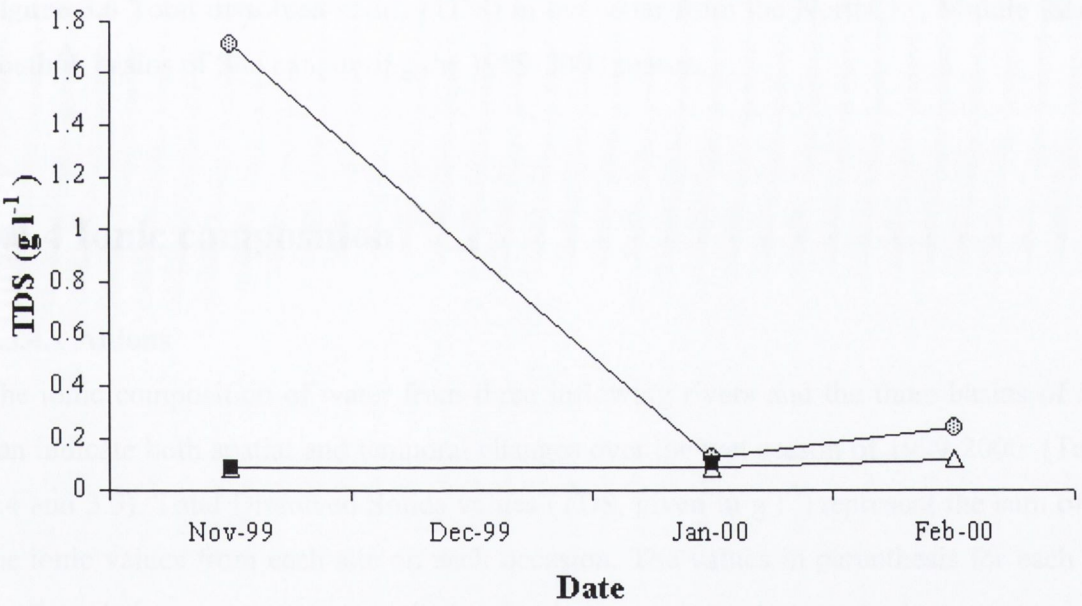


Figure 3.5 Total dissolved solids (TDS) in the water from the Nata ⊙ , Mosetse △ and Semowane ■ rivers that run into the north and middle basins of Sua pan, during the 1999-2000 wet season.

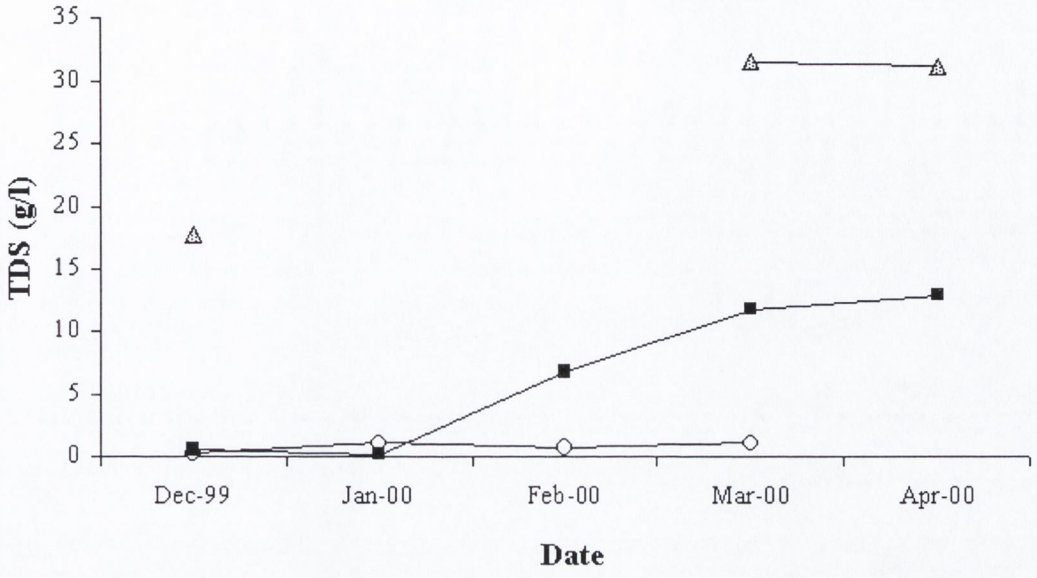


Figure 3.6 Total dissolved solids (TDS) in the water from the North○ , Middle ■ and South△ basins of Sua pan, during the 1999-2000 season.

3.3.4 Ionic composition

3.3.4.1 Anions

The ionic composition of water from three inflowing rivers and the three basins of Sua pan indicate both spatial and temporal changes over the wet season of 1999-2000 (Table 3.4 and 3.5). Total Dissolved Solids values (TDS, given in g l^{-1}) represent the sum of all the ionic values from each site on each occasion. The values in parenthesis for each ion are the relative percentage equivalents of cations or anions. Among the important anions, Cl^- and HCO_3^- were generally dominant. River water contained low percentages of Cl^-, ranging from 6% to 22% of the total anion composition. It was, however, the dominant anion (61%) in the first discharge waters of the Nata River. In the basin lakes, Cl^- ions were less abundant in the first few months of flooding, in the North and Middle basins, but later increased, ranging from 12% to 91% of the total anions, and became the dominant anion as salinity increased. HCO_3^- was more abundant in the fresher waters of the basins, ranging from 2% to 87% of anions and decreased with increasing salinity. It

was the dominant anion in river waters, ranging from 74 to 90%. In November, it comprised only 32% of total anions in the Nata River. Despite large changes in the proportions of Cl^- and HCO_3^-, SO_4^{2-} varied relatively little in its proportion of the total anionic composition as salinity increased and ranged from 2.5% to 4% in the rivers and 1.4% to 6.6% in the basin lakes. The pattern of anion dominance in the rivers was $HCO_3^- > Cl^- > SO_4^{2-}$ (88% of the time) and $Cl^- > HCO_3^- > SO_4^{2-}$ (58% of the time) in the basins. At the beginning of the 1999-2000 season, however, the anionic dominance pattern was $HCO_3^- > Cl^- > SO_4^{2-}$ in the north and middle basins.

3.3.4.2 Cations

Among the cations, Na^+ was the dominant ion in the basin waters, while the proportions of the divalent cations K^+ and Ca^{2+} were generally higher in river waters (Table 3.4 & 3.5). The Semowane and Mosetse rivers contained little Na^+, with percentages ranging from 8% to 29%. Na^+ was the dominant cation in the Nata River at the beginning of the season and decreased from 92% to 16% as the season progressed. It was by far the most dominant cation recorded in the basin waters, ranging from 70% to 94% of total cations and became more dominant with increasing evaporative concentration, as the floods dried up. K^+ ranged from 5% to 20% of cation composition in the rivers and from 4 to 11% in the basins. Unlike Na^+, K^+ did not show any major change in its proportion of total cation composition with increased salinity. The divalent cations Ca^{2+} and Mg^{2+} did, however, decrease with increasing salinities and disappeared completely in the south basin at the highest salinities recorded. In contrast, Ca^{2+} was one of the most abundant cations in the rivers, ranging from 2% to 47%. Mg^{2+} ions were not as abundant and ranged from 0.6% to 9% of cation composition. Si^+ ions made up a substantial proportion of the cations in both river and basin waters and, sometimes, exceeded Mg^{2+} and K^+ ions as the second most dominant cation. Similarly, among the basins, it was often the second most abundant cation (after sodium), ranging from 1 to 14% of the total cation composition. It rapidly decreased, however, relative to Na^+ as TDS increased in the middle and south basins. The patterns of cation dominance in the rivers was $Ca^{2+} > K^+ > Na^+ > Mg^{2+}$ (63% of the time), and $Na^+ > K^+ > Ca^{2+} > Mg^{2+}$ (25%). Cation dominance in the basin waters of Sua pan was $Na^+ > K^+ > Ca^{2+} > Mg^{2+}$ (92% of the time).

Other trace metals present in small quantities in the results but not listed in Tables 3.4 and 3.5 were the cation Sr^{2+} and the anion Br^-. Sr^{2+} ranged between 0.06 and 0.18 mg l^{-1} in the rivers (< 0.4% of the cation composition) and between 0.02 and 0.25 mg l^{-1} in the basins (< 0.1% of the cation composition). Br^- was present mostly at <0.05 mg l^{-1} but in November it was present at 1.7 mg l^{-1} in the Nata river. Results ranged from 0.06 to 42 mg l^{-1} in the basin waters, the highest values occurring in the highly saline south basin as values increased with TDS. It failed, however, to exceed 0.2% of anion composition.

Table 3.4 Ionic composition of three inflowing rivers, Nata, Mosetse and Semowane, during the 1999-2000 wet season, with TDS in g l^{-1} and individual ion concentrations in mg l^{-1}. Values in parenthesis are percentage equivalents of cations or anions.

Locality	Date	TDS	Na^+	K^+	Ca^{2+}	Mg^{2+}	Si^-	Cl^-	HCO_3^-	SO_4^{2-}
Nata River	Nov	1.71	560	30	11	3.9	5.5	670	350	75
			(91.7)	(4.9)	(1.8)	(0.6)	(0.9)	(60.9)	(31.8)	(6.8)
	Jan	0.12	6.4	8.1	14	3.1	8.4	6.8	75	2.1
			(15.9)	(20.2)	(34.9)	(7.7)	(20.9)	(8)	(87.9)	(2.5)
	Feb	0.24	35	7.6	22	4.3	9.5	35	120	6.2
			(44.5)	(9.7)	(28)	(5.5)	(12.1)	(21.5)	(73.6)	(3.8)
Semowane R.	Nov	0.09	2.2	5.3	13	2.6	5.5	4.8	55	2.3
			(7.7)	(18.5)	(45.3)	(9.1)	(19.2)	(7.7)	(88)	(3.7)
	Jan	0.1	3	6.1	14	2.7	4.11	4.8	65	2.1
			(9.9)	(20.3)	(46.6)	(9)	(13.7)	(6.4)	(87.4)	(2.8)
Mosetse River	Nov	0.09	4.1	5.6	10.5	2.6	5.4	4.9	50	2.6
			(14.5)	(19.8)	(37)	(9.2)	(19)	(8)	(83)	(4.3)
	Jan	0.086	8.3	5.7	8.4	1.6	4.4	9.3	45	2.4
			(29)	(20)	(29.5)	(5.6)	(15.5)	(16)	(77.4)	(4.1)
	Feb	0.012	4.6	5.6	16	3.3	6.1	5.8	75	2.5
			(13)	(15.7)	(44.8)	(9.2)	(17)	(6.9)	(89.6)	(3)

Table 3.5 The ionic composition of the North, Middle and South basins of Sua pan during the 1999-2000 wet season, with TDS in g l^{-1} and individual ion concentrations in mg l^{-1}. Values in parenthesis are percentage equivalents of cations or anions.

Locality	Date	TDS	Na^+	K^+	Ca^{2+}	Mg^{2+}	Si^-	Cl^-	HCO_3^-	SO_4^{2-}
North Basin	Dec	0.26	65	9.8	4.4	0.5	12.8	55	105	5.8
			(70.2)	(10.6)	(4.8)	(0.5)	(13.8)	(33)	(63.3)	(3.5)
	Jan	1.1	335	25	5.2	0.37	24	360	300	29
			(86)	(6.4)	(1.3)	(0.1)	(6.2)	(52)	(43.4)	(4.2)
	Feb	0.7	205	19	10.3	1.1	17	210	220	24
			(81)	(7.5)	(4.1)	(0.4)	(6.7)	(46)	(48)	(5.3)
	Mar	1.12	365	27	6.5	0.79	24	425	240	35
			(86.2)	(6.4)	(1.5)	(0.2)	(5.7)	(60.6)	(34.2)	(5)
Middle Basin	Dec	0.58	175	8.4	8.8	0.8	11.6	180	185	11
			(85.5)	(4.1)	(4.3)	(0.4)	(5.7)	(47.6)	(49)	(2.9)
	Jan	0.23	55	6.4	2.3	0.14	9	18	135	2.2
			(75.4)	(8.8)	(3.2)	(0.2)	(12.4)	(11.6)	(87)	(1.4)
	Feb	6.75	2550	150	4.8	0.05	38	3600	155	250
			(93)	(5.5)	(0.2)	(0.01)	(1.4)	(89.7)	(3.9)	(6.2)
	Mar	11.8	4300	230	4.25	0.05	55	6250	475	475
			(93.7)	(5)	(0.1)	(0.01)	(1.2)	(86.6)	(6.6)	(6.6)
	Apr	12.9	4800	400	3.4	0.05	58	7000	160	500
			(91.2)	(7.6)	(0.1)	(0.01)	(1.1)	(91.2)	(2.1)	(6.5)
South Basin	Dec	17.8	6500	350	2.25	0.4	215	8500	1800	380
			(92)	(5)	(<0.01)	(<0.01)	(3)	(79.4)	(16.8)	(3.6)
	Mar	31.5	11500	650	3.7	0.009	140	16400	1770	1050
			(93.5)	(5.3)	(0)	(0)	(1.1)	(85.1)	(9.2)	(5.4)
	Apr	31.2	11500	600	4.9	0.035	125	16000	1700	1200
			(94)	(4.9)	(0)	(0)	(1)	(84.4)	(9)	(6.3)

The correlation between TDS and equivalent conductivity results from the same sampling dates was strong one (r = 0.998, n = 12, $P \leq 0.001$; variables square-root transformed) (Fig. 3.7).

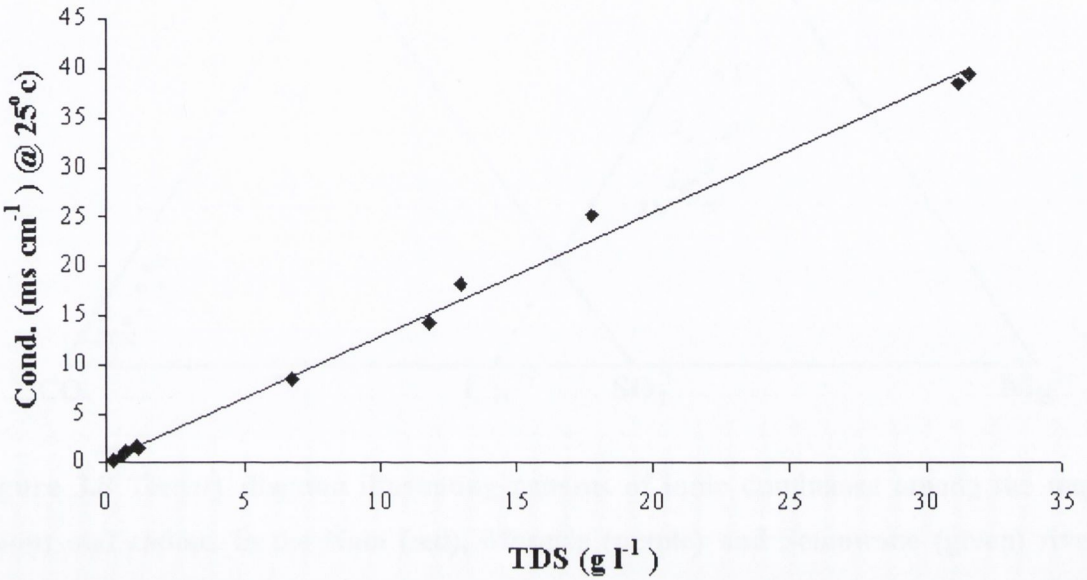


Figure 3.7 Relationship between TDS and Conductivity in the waters of Sua Pan, during the 1999-2000 season, with the line of best fit shown.

Changes in the relative proportions of the major cations and anions in the rivers and basins are illustrated in ternary diagrams (Fig 3.8 & 3.9). The ionic proportions in the Mosetse and Semowane rivers indicated the waters to be, predominantly, sodium - calcium carbonate waters, containing similar proportions of sodium and calcium (Fig. 3.8). Nata River, however, clearly contained sodium chloride waters at the beginning of the season, but contained sodium – calcium carbonate waters in January and changed again to a sodium carbonate-chloride composition. From the ternary diagrams the sodium carbonate -chloride waters fill the north and middle basins at the beginning of the 1999-2000 wet season, but otherwise floodwater on Sua pan can be classified as sodium chloride, with the major ions, sodium and chloride comprising high percentages of the total cationic and anionic composition, respectively (Fig. 3.9).

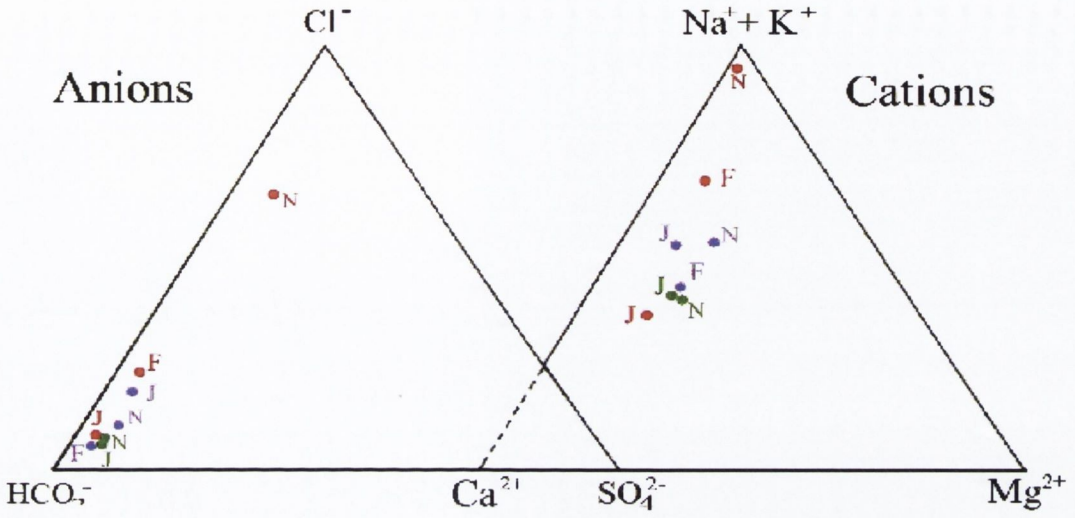


Figure 3.8 Ternary diagram illustrating patterns of ionic dominance among the major anions and cations in the Nata (red), Mosetse (purple) and Semowane (green) rivers. Plots are based on equivalent percentages of ions in g l^{-1}. Apices indicate 100 % equivalent of anions/cations. Values are labelled according to monthly samples taken in November (N), January (J) and February (F).

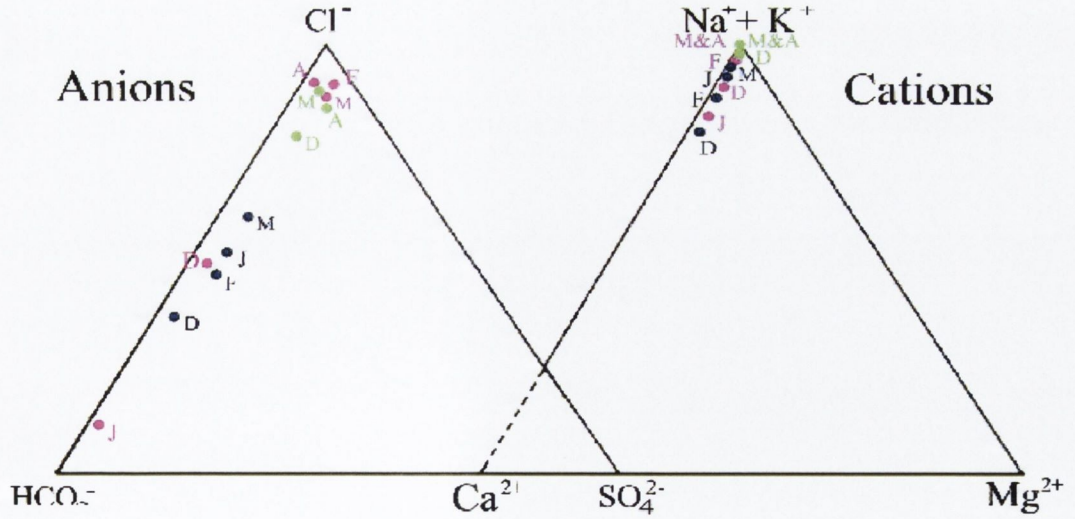


Figure 3.9 Ternary diagrams illustrating the patterns of ionic dominance among the major anions and cations in the north (blue), middle (pink) and south (green) basins. Apices indicate 100 % equivalent of ions in g l^{-1}. Values labelled according to the monthly samples taken in December (D), Jan (J), Feb (F), March (M) and April (A).

A change in the relative proportions of major cations and anions was observed as TDS increased on Sua pan (Fig. 3.10). Dominant anions changed from HCO_3^- to Cl^-, with increased salinity. It is also clear that, while Na^+ was the dominant cation, Ca^{2+} did exist, at relatively high proportions, in lower salinities. Ca^{2+} loss to precipitation occurred rapidly above salinities of 1.12 g l^{-1} and was detected in solution at very low concentrations ≥ 6.7 g l^{-1}. A linear trend represents the rate of Ca^{2+} ion precipitation (Fig 3.10). Similarly, the ratio of Cl^- : Cl^- + HCO_3^- shows a progressive increase in Cl^- ions and a decrease in HCO_3^- ions with increased salinity levels. By far the dominant anion at low salinity was HCO_3^-, but as salinity increased the proportion of Cl^- ions increased. A decrease in HCO_3^- ions occurred gradually (illustrated by the curved line on the plot below), but loss through precipitation increased above 1.12 g l^{-1}. Bicarbonate ions are then rapidly lost and become a small percentage of the cation composition. Higher bicarbonate concentrations in the south basin, where maximum TDS was recorded, were associated with an absence of calcium ions.

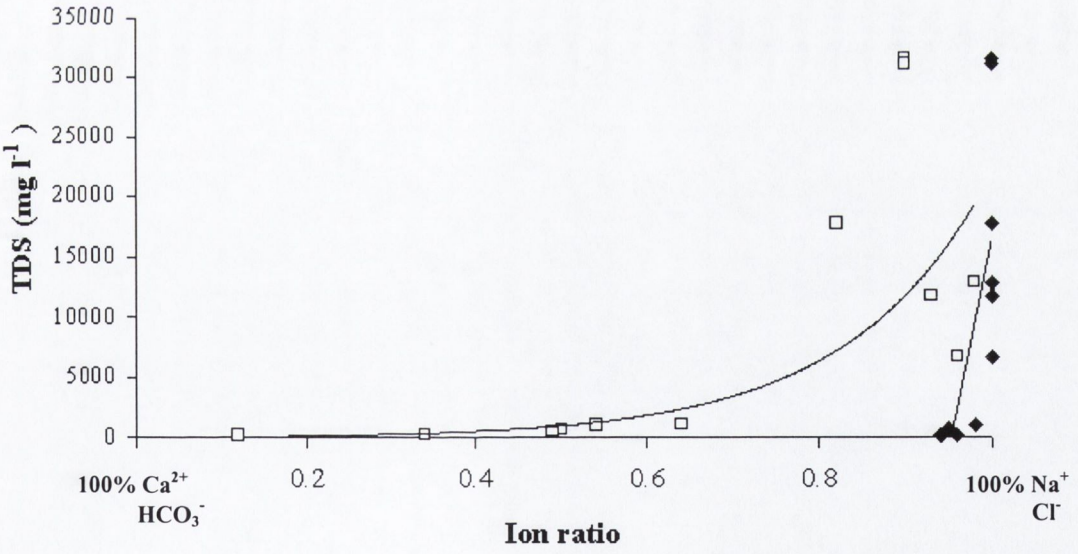


Figure 3.10 The ratio of Na^+ : Na^+ + Ca^{2+}, □ and Cl^- : Cl^- + $HCO3^-$, ◆ plotted against the TDS values for the north, middle and south basins. Curvilinear line represents the trend of increase in Cl^- with increased TDS and the linear line represent the precipitation rate of Ca^{2+} with increased TDS.

3.3.5 Phosphorus and Nitrogen

Total phosphorus in the north basin ranged between 0.18 (0.006 mmol l^{-1}) and 0.44 mg l^{-1} (0.014 mmol l^{-1}) and in the middle basin, ranged from 0.04 (0.0013 mmol l^{-1}) to 0.52 mg l^{-1} (0.017 mmol l^{-1}) before it dried out (Fig. 3.11). Concentrations in the south basin were higher and showed an even greater increase in concentration from 0.62 to 2 mg l^{-1} (0.02 to 0.065 mmol l^{-1}) over three weeks, before it too dried out. TDP results, in general, varied somewhat from TP results and ranged from 0.13 to 0.23 mg l^{-1} (0.004 to 0.007 mmol l^{-1}) in the north basin, 0 to 0.47 mg l^{-1} (0 to 0.015 mmol l^{-1}) in the middle basin and 0.62 to 2mg l^{-1} (0.02 to 0.065 mmol l^{-1}) in the south basin (Fig. 3.11).

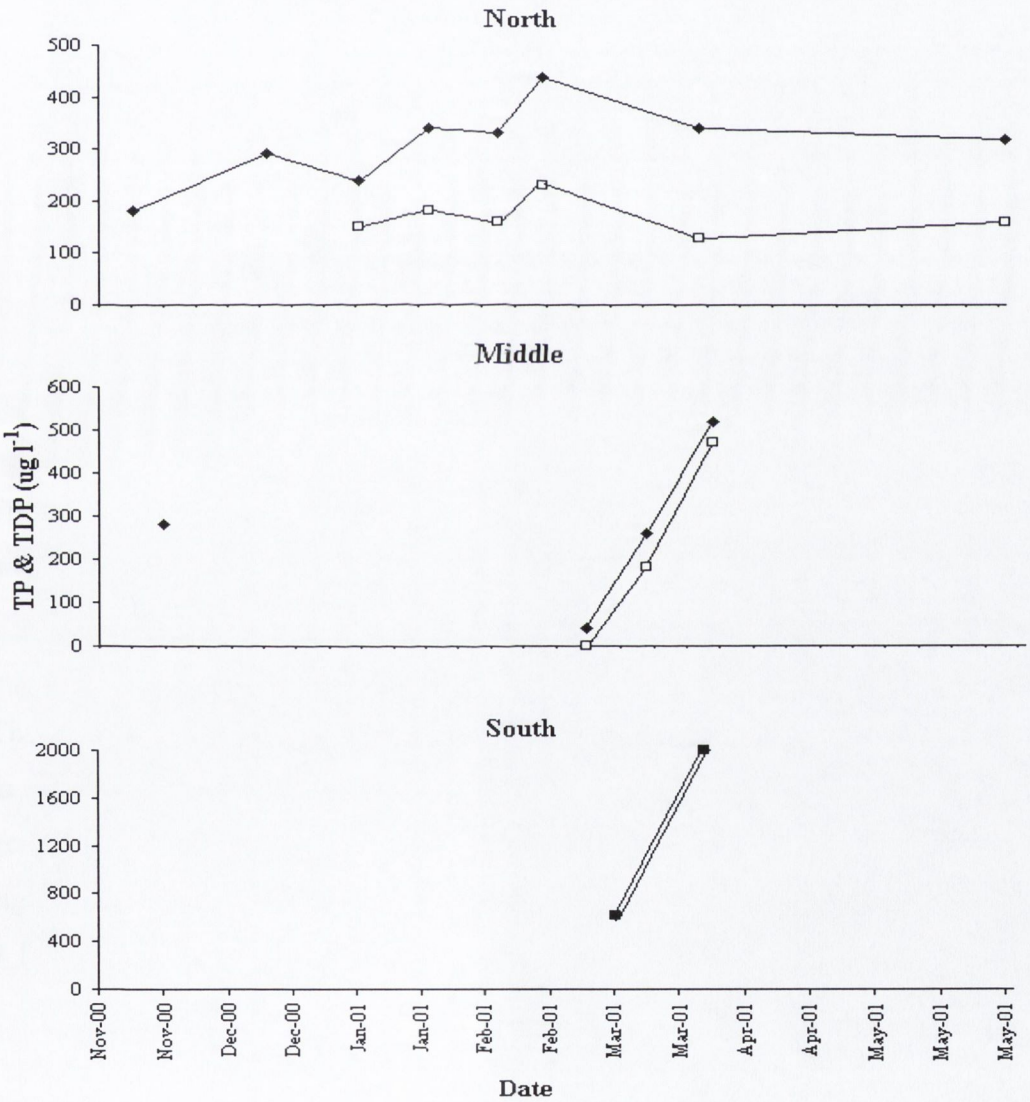


Figure 3.11 TP ◆ and TDP□ in the north, middle and south basins, during 2000-2001.

Total phosphorus showed a close correlation with conductivity in the lake waters from all three basins ($r = 0.97$, n = 14, $P \leq 0.001$; variables square-root transformed) (Fig. 3.12). It should be noted, however, that the correlation r value is heavily influenced by a single point representing the relationship at highest conductivity and TP concentration and introduces heterodiscosity into the relationship.

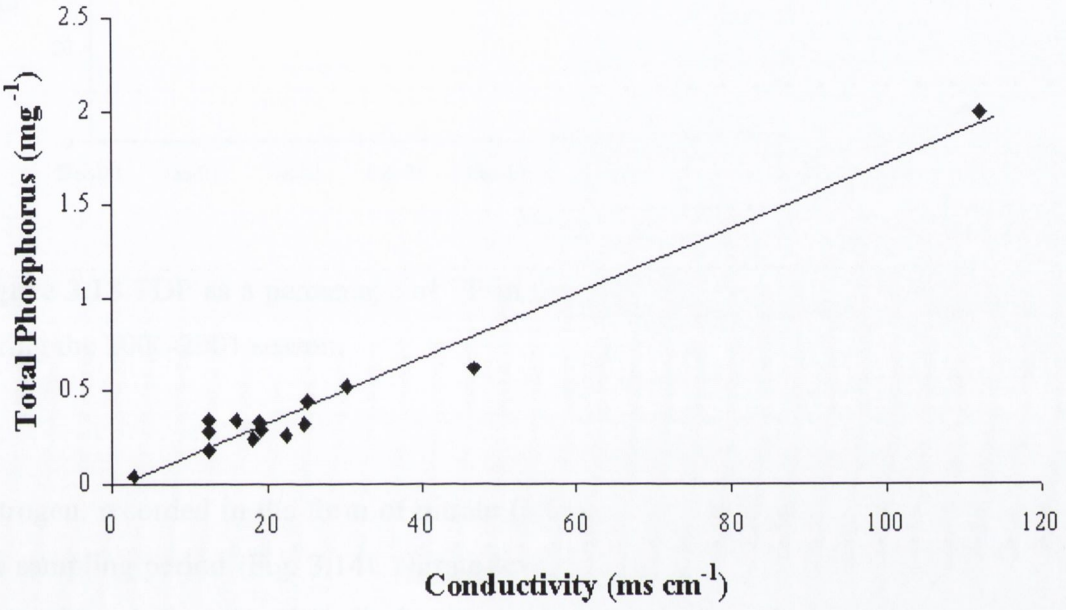


Figure 3.12 Relationship between total phosphorus (TP) and conductivity on the north, middle and south basins during the 1999-2000 wet season, with the line of best fit shown.

The proportion of TDP to TP varied between 38 and 63% in the north basin, 49 and 90% in the middle basin and accounted for total TP (100%) in the south basin (Fig. 3.13). In general, the proportion of TDP to TP increased as the lakes dried up and there is a significant correlation between the proportion of TDP to TP and conductivity ($r = 0.76$, n = 11, $P = 0.01$; variables square-root transformed).

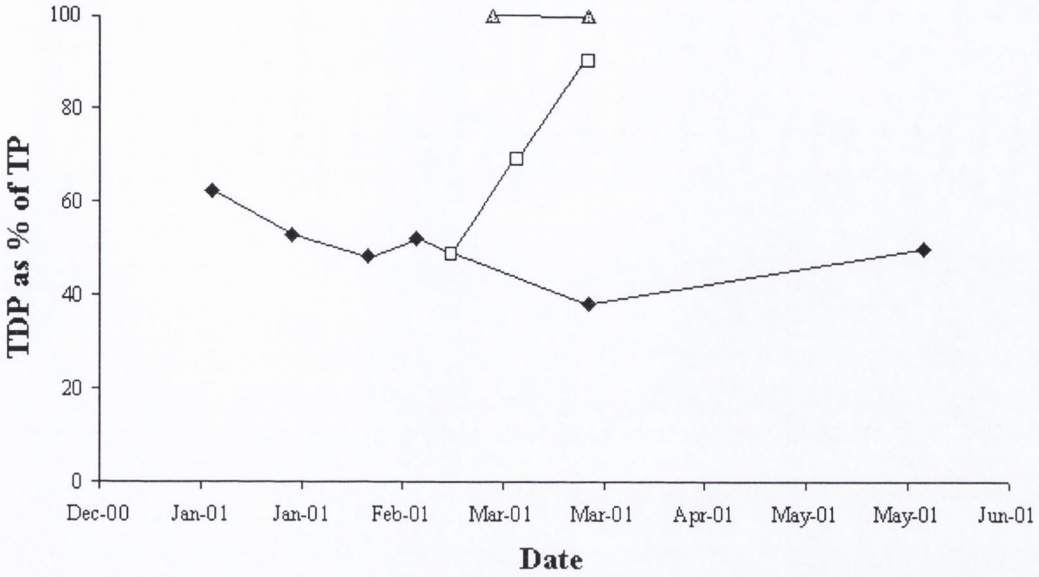


Figure 3.13 TDP as a percentage of TP in the north ◆, middle □ and south △ basins during the 2000-2001 season.

Nitrogen, recorded in the form of nitrate (NO_3-N), in the rivers showed a decrease over the sampling period (Fig. 3.14). Nitrate levels in the Nata River were at their highest in November, during the first discharge event (3.3 mg l^{-1}). Levels then decreased with continuous discharge and values dropped to 0.7 mg l^{-1} in February. Similarly, concentrations in the Mosetse River also decreased over time, from 2.9 mg l^{-1} in November to 0.4 mg l^{-1} in February. Results from the Semowane River, however, increased from 0.4 mg l^{-1} in November to 2.4 mg l^{-1} in January.

Total nitrogen in the three basins also showed spatial and temporal variation (Fig. 3.15). TN values in the north basin oscillated but there was a general increase from 2.6 mg l^{-1} (0.19 mmol l^{-1}) to 6.3 mg l^{-1} (0.45 mmol l^{-1}) between November 2000 and June 2001. TN decreased in the middle and south basins from, respectively, 3 mg l^{-1} to 1.4 mg l^{-1} (or 0.21 to 0.1 mmol l^{-1}) and 2.2 mg l^{-1} to 2 mg l^{-1} (or 0.16 to 0.14 mmol l^{-1}). No significant relationship was found between conductivity and TN.

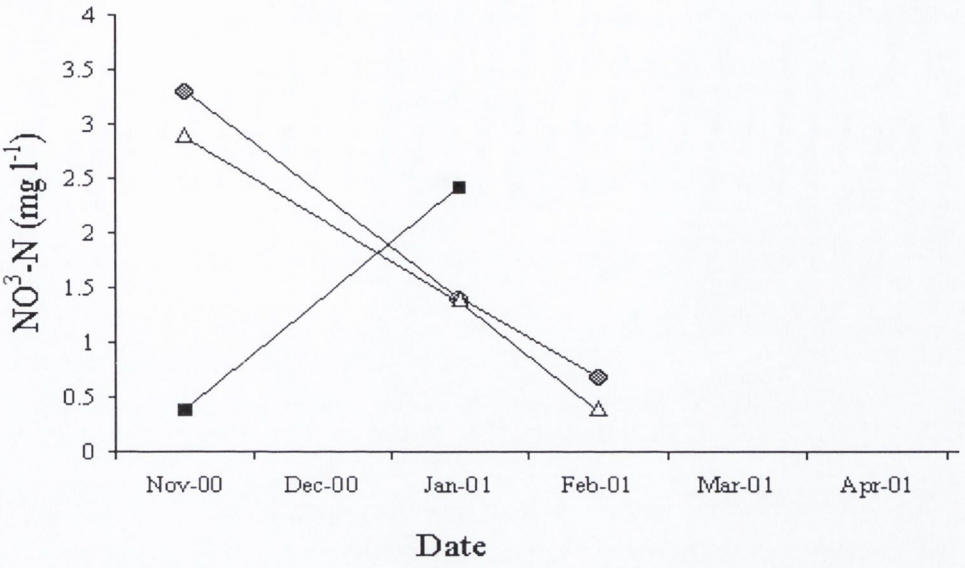


Figure 3.14 Concentration of NO_3^- load in discharge waters of the Nata ◍, Mosetse△ and Semowane■ rivers, from November 2000 to February 2001.

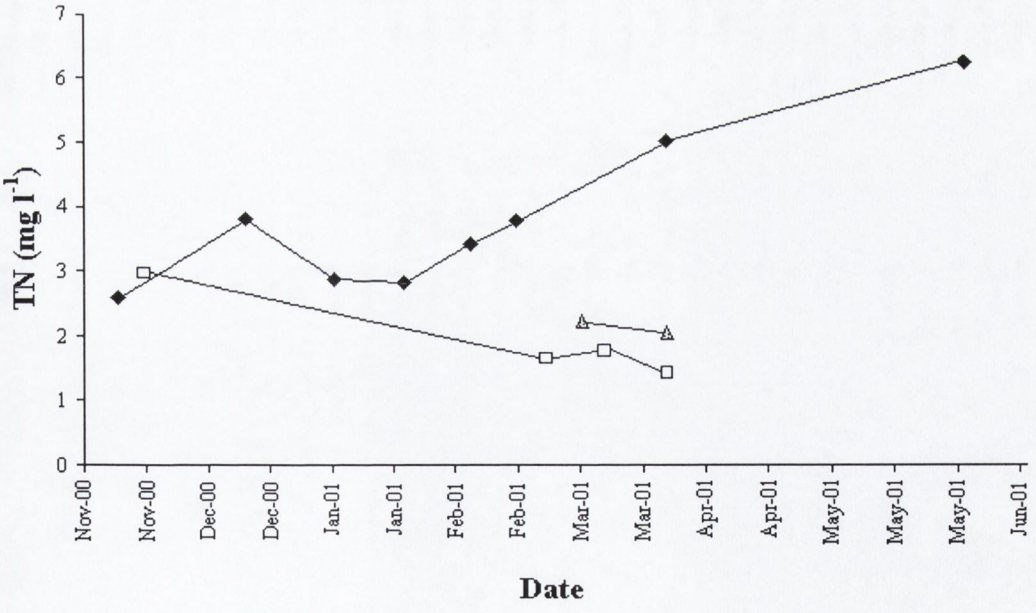


Figure 3.15 Concentration of TN in the north ◆, middle □ and south △ basins, from November 2000 to June 2001.

The ratio of nitrogen to phosphorus in the north, middle and south basins decreased, in a gradient from north to south (Fig. 3.16). In the north basin, the ratio decreased from 32, in November 2000, to 19, in late January, before increasing again to a maximum recorded ratio of 43 at the end of the season. The ratio decreased from 24 to 6 in the middle basin, and from 8 to 2 in the south basin, during respective flood periods.

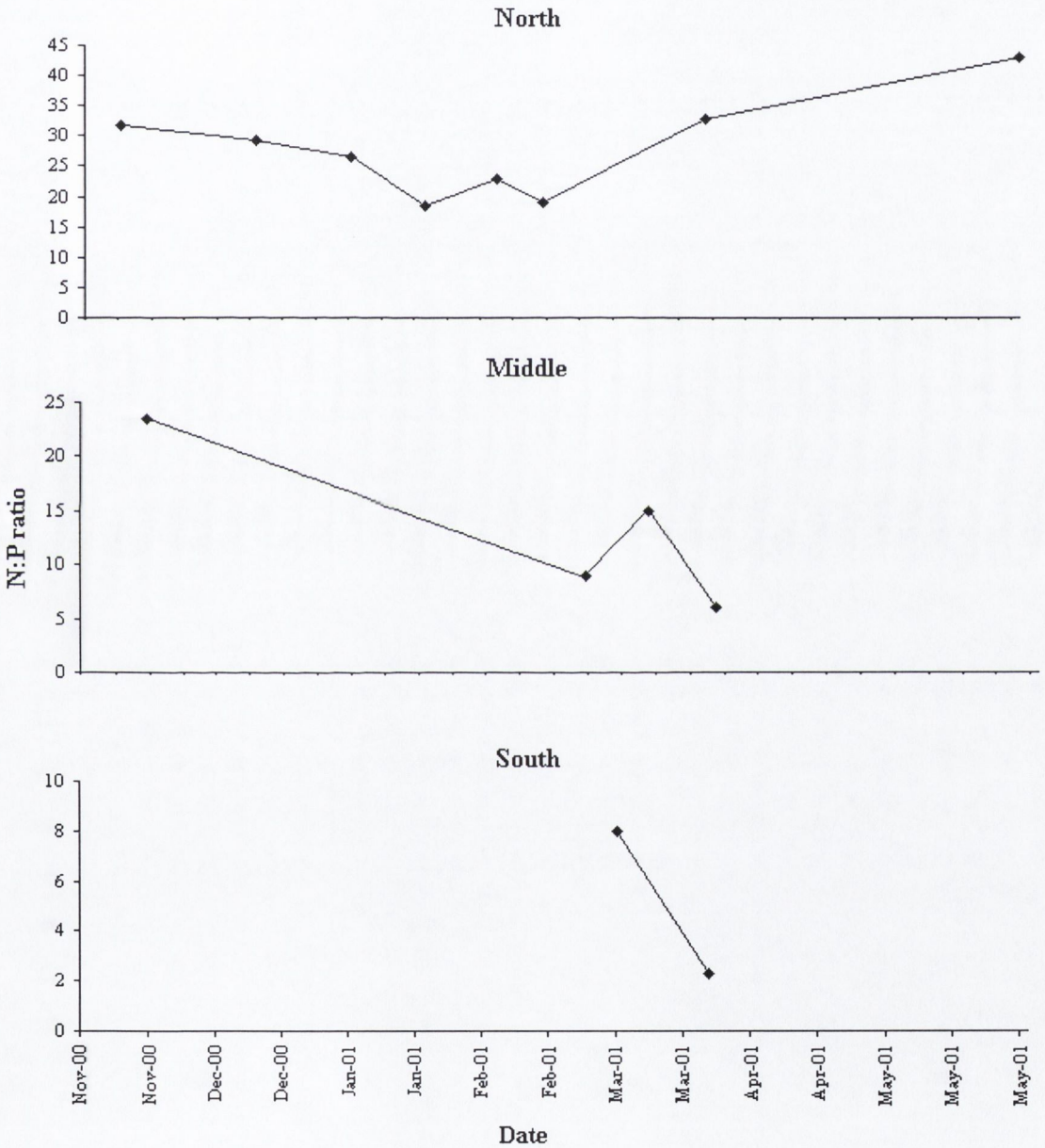


Figure 3.16 N:P ratio in the north, middle and south basins during the 2000-2001 wet season.

3.4 Discussion

3.4.1 Salinity variability

Salinity is one of the most important chemical factors controlling the composition of the plant and animal communities in African saline lakes (Talling & Talling, 1965; Kilham, 1971; Hecky & Kilham, 1973; La Barbera & Kilham, 1974; Vareschi, 1978, Seaman *et al.*, 1991; Allan *et al.*, 1995). The survival of many species in saline lakes appears to be related to the total concentrations of ions rather than their proportions (Hutchinson *et al.*, 1932; Bayly & Williams, 1966; Hartland-Rowe, 1966). Large intra-seasonal variation in salinity also imposes limitations on the biological composition in temporary waters (Hartland-Rowe, 1972; Williams, D.D., 1987; Williams, 1998). From the conductivity results, it is clear that there were large spatial and temporal variations in the salinity of the lake waters of Sua pan. A close correlation between conductivity and TDS on Sua pan is consistent with the generally found linear relationship that conductivity increases as the numbers of ions increase (Williams & Sherwood, 1994) (Fig. 3.6). Conductivity results indicate a distinct salinity gradient from north to south (Fig. 3.2), with water in the north basin relatively low in salinity during the 1999-2000 wet season. Indeed, the seasonal maximum conductivity in the north basin (1.78 mS cm^{-1}) was below the saline lake boundary level of 3 g l^{-1} (~ 6 mS cm^{-1}) set by Williams (1964) owing to the large amounts of freshwater that flowed onto the north basin during that season (Chapter 2). Low saline conditions prevailed despite higher salt concentrations measured in the Nata River during initial discharge period (Fig. 3.5). During the 2000-2001 wet season, when evaporative concentration increased and the ionic concentration increased to a seasonal maximum of 25.5 ms cm^{-1}, it still remained less saline than the middle and south basin waters. The rapid increase in salinity in the middle and south basins, after initial flooding, can be contributed to the influence of dissolving salts from the pan sediment efflorescence (Shaw & Thomas, 1989; Thomas & Shaw, 1991). The south basin appeared to be the most porous of the three basins (the softest) which would facilitate more evaporative 'pumping' of the ground water and the deposition of large amounts of

efflorescence on its surface. This was visibly the case when the pan was observed from the air during the end of the wet seasons. Salinity increased at a faster rate than the middle pan, perhaps, as a result of the broad shallow nature of the lake and the resulting higher areal evaporation rates. It may also have been under greater influence from rising groundwater, resulting in higher solute loading (Eugster & Hardie, 1978; Shaw & Thomas, 1989). Notwithstanding this, salinities in the south basin are among the highest recorded of any saline lake in Africa (Talling & Talling, 1965; Day, 1993; Seaman *et al.*, 1991). The last samples of the 1999-2000 season were taken, respectively, five weeks and eight weeks before the middle and south basins dried up and maximum salinities were, therefore, likely to have been substantially higher before the basins dried completely. Given the fact that the north basin receives more flood water and floods for longer periods than the middle and south basins (Chapter 2), it is likely that the north basin is consistently less saline, ensuring the presence of a salinity gradient on Sua pan throughout each wet season.

3.4.2 Origins of salinity and solute dominance on Sua pan

The patterns of anion and cation dominance in the lakes of Sua pan are different from the majority of saltpans around southern Africa. Among the cations, K^+ was generally more abundant than Ca^{2+} and Mg^{2+}, while the opposite is the case for the majority of saline waters in southern Africa (Seaman *et al.*, 1991; Day, 1993). The patterns of ion dominance in these results are more consistent with those from Pretoria Salt Pan (Ashton & Schoeman, 1983), Etosha Pan (Berry, 1972), and some other inland temporary saline pans (Seaman *et al.*, 1991), where bicarbonate ions are more abundant. Indeed, HCO_3^- ions are the most dominant ions in the less saline waters during the initial stages of flooding. The origins of these ions in similar salt lakes are derived from the catchment and or substratum of the lake (Shaw & Thomas, 1989; Kilham, 1990; Seaman *et al.*, 1991; Day, 1993). TDS results for three rivers that flow into Sua pan indicate that the salinity in the basin lakes is influenced by freshwaters from the catchments. The cationic

composition of the Mosetse and Semowane rivers (Fig 3.8) are consistent with ionic compositions of the majority of freshwaters in southern Africa (Day, 1993). This may be owing to the influence of $CaCO_3$ deposits in the catchments, which is a common characteristic in the area around the Makgadikgadi pans (Thomas & Shaw, 1991). $CaCO_3$ (calcrete) can contribute up to 70% of the mineral content of the soil/rock structure in the Nata area (Gwosdz & Modisi, 1983). High proportions of Ca^{2+} and HCO_3^- ions occurred in the north and middle basins, during the months of December and January. Water from the Nata River, however, differed in ionic composition compared with waters in the other rivers and contained salinities (240 to 1710 mg l^{-1}) that exceeded estimates of 156 mg l^{-1} reported by Gould (1980) for the same river. Na^+ and Cl^- ions were abundant in November 1999, during initial discharge, and high concentrations of these ions suggest an input from the weathering of rocks rich in chlorides and carbonates of Na^+ and Ca^{2+} (Stumm & Morgan, 1970; Eugster & Hardie, 1978). It could also be owing to the fact that the Nata River has a very large catchment and a number of dams and large pools of standing water along its course. These standing water bodies can persist throughout the year and their chemical composition is likely to be influenced by evaporative concentration, which favours sodium and chloride dominance, with salinities of 1.4 g l^{-1} (1,365 ppm), to 34 g l^{-1} (~ 34,030 ppm) (Berry, 1972). There was, however, a large influence of river water on the north and middle basin salinity, which can be determined by the high proportions of Ca^{2+} and HCO_3^- ions in the basins waters at the beginning of the seasons, when the rivers were flowing. High concentrations of Na^+ and Cl^- in the middle and, particularly, the south basins suggest a large proportion of the ionic composition of these waters must originate from the dissolution of evaporates on and in the subsurface layers of the pan sediment and from the highly saline ground water that lies just beneath the surface.

According to Gibbs (1970), changes in the relative ratios of the major anions and cations with increased salinity, reveals something about the major factors controlling the chemical composition of these waters. Plotting the changes in the ratios of $Na^+ : Na^+ + Ca^{2+}$ and $Cl^- : Cl^- + HCO_3^-$ with an increase in TDS illustrates the behaviour of the major ions over the flood period and indicates whether the chemical composition is determined

by minerals derived from the weathering of rocks ('rock dominance') or by evaporative concentration ('evaporative dominance'). The relative ratios of the major cations and anions in the basins of Sua pan changed considerably each season (Fig. 3.10). High proportions of HCO_3^-, associated with relatively high percentages of Ca^+ ions in initial floodwaters, suggested ionic composition was influence by dissolved minerals derived from the weathering of rocks in the catchment. The change in composition to Na^+ and Cl^- dominated waters as salinity increases, occurs as a direct result of evaporative concentration because HCO_3^- and Ca^{2+} and Mg^{2+} ions are lost to precipitation of their combination minerals (Gibbs, 1970). As salinity increased in Sua pan, the effect of evaporative concentration is clearly evident (Fig 3.10). It appears that rapid Ca^{2+} precipitation begins at low salinities (1.12 g l^{-1}), which may be owing to the large amounts of bicarbonate in solution (Day, 1993). Relatively high concentrations of bicarbonate ions in the south basin, where salinities were highest, were associated with low to only trace amounts of Ca^{2+} ions. When salinities increase, bicarbonate remains relatively high in the absence of cations such as Ca^{2+}, with which they bind and precipitate out of solution (Eugster & Hardie, 1978). Further precipitation of bicarbonate with Mg^{2+} (to form $MgCO_3$) may have continued to reduce the relative proportions of bicarbonate at a slower rate (Stumm & Morgan, 1970; Eugster & Hardie, 1978).

Silica concentrations were not as high as those recorded in many East African lakes (Talling & Talling, 1965) and precipitation also occurred at higher salinities in the middle and south basins, which reduced concentrations to relatively low levels. This process is common at high salinities, in association with the loss of Ca^{2+} and Mg^{2+} ions, in the formation of calcium and magnesium silicates (Hutchinson, 1957; Thomas & Shaw, 1991). Indeed, it may have contributed to layers of silcrete that contribute to the underlying geology of the area (Shaw *et al.*, 1988; Shaw and Thomas, 1989). Silica is also removed from the water by diatoms (Talling, 1966; Eugster & Hardie, 1978; Horne & Goldman, 1994) and may be accelerated in very shallow saline lakes where diatoms are abundant (Hecky & Kilham, 1973; Tuite, 1981; 2000). Concentrations are, however, unlikely to be low enough to limit diatom growth and production.

3.4.3 pH

High pH in the three basins of Sua pan are consistent with high values reported in similar saline lakes around southern Africa rich in $HCO_3^- + CO_3^{2-}$ ions (Hutchinson *et al.*, 1932, Berry, 1972, Ashton & Schoeman, 1983; Seaman & Kok, 1987). Among the three basins, however, different patterns of change over the coarse of both wet seasons were observed (Fig 3.3). Frequent short-term fluctuations in pH may have be attributed to frequent changes in the uptake and production of inorganic carbon as a result biological activity, which varies diurnally (Wetzel & Likens, 1990; Wetzel, 2001). The values for the north basin were the lowest and fluctuated considerably. The large fluctuations in values can be attributed to the relative changes in H_2CO_3 and HCO_3^- coming into the lake from the Nata and Semowane rivers and fluctuating rates of CO_2 uptake by photosynthesis (Meintjes *et al.*, 1994). The steady increase in values in the 2000-2001 season can be attributed to an increase in conductivity over that season. A significant correlation between these two parameters for the north basin is consistent with this phenomenon (Fig. 3.4). The pH values for the middle basin were generally higher in the 1999-2000 season and increased with conductivity. This association appears to reach an asymptote in the 2000-2001 season, however, as values remain between 9.5 and 10 with further increases in conductivity. Similarly, the high pH in the south basin remained fairly constant during the 1999-2000 season, despite large increases in salinity, and decreased during the 2000-2001 season as salinity increased even higher. pH, therefore, appeared to increase with conductivity to between 9.5 and 10 but further increases in conductivity beyond approximately 60 ms cm^{-1} resulted in an asymptotic relationship and a subsequent decrease. This is consistent with decreases in pH with very high salinities observed in other highly saline lakes, explained by changes in the dissociation - association processes of the carbonate equilibrium; at very high salinities and where CO_3^- is the important alkali, pH decreases with further ionic concentration (Hammer, 1986; Stumm & Morgan, 1970). Rapid precipitation of $CaCO_3$ at high salinities also removes $HCO_3^- + CO_3^{2-}$ ions from solution and alters the pH equilibrium in favour of slightly more acidic conditions, as HCO_3^- & CO_3^{2-} are reduced and CO_2 is produced during the process (Stumm & Morgan, 1970). The opposite may be the case at the beginning of the rainy seasons when

initial flooding dissolves surface trona efflorescence (Na_2CO_3 - Na_2HCO_3 - $2H_2O$) and, more importantly, $CaCO_3$, resulting in a large imparting of HCO_3^- and CO_3^{2-} into solution and a withdrawal of CO_2 and H_2CO_3 from solution (Stumm & Morgan, 1970). This initial bias in the carbonate equilibrium in favour of the these alkaline bases, with a withdrawal of dissolved CO_2, may account for the higher pH values recorded at the beginning of the 1999-2000 and 2000-2001 floods (Fig. 3.3 & 3.4). It was likely that pH has a major influence on the flora and fauna communities that exist in the waters of Sua pan. High pH can inhibit the existence of many species of plant and animals (e.g. Hecky & Kilham, 1973; La Barbara & Kilham, 1974). At elevated pH, ammonium, for example, may change its ionic form to ammonium hydroxide (NH_4 OH), which is toxic to many plants and animals (Horne & Goldman, 1994).

3.4.4 Nutrients

The concentration of phosphorus in temporary saline lakes is frequently high owing to large inputs from seasonal river runoff, lake sediment regeneration and from the activities of animals and birds (Prowse & Talling, 1958; Moss & Moss, 1969; Livingstone & Melack, 1984). Under tropical & semi-tropical conditions, that favour high temperature and light availability, temporary saline lake ecosystems can, therefore, be highly productive (Hartland-Rowe, 1972; Talling & Lemoalle, 1998). Concentrations of TP in the lakes of Sua pan (180 – 2000 $\mu g\ l^{-1}$) are among the highest estimates from saline and alkaline rich lakes around southern and East Africa (Talling & Talling, 1965; Prosser *et al.*, 1968; Melack, 1978; Ashton & Schoeman, 1983). A large population of flamingos that migrate to Sua, to feed and breed (Chapter 6) provide important potential for nutrient loading from initial droppings and the subsequent rapid recycling of nutrients 'locked up' in the food chain (Vareschi, 1978; Livingstone & Melack, 1984). Indeed, some of the highest TP concentrations recorded in African lakes come from shallow soda lakes, on which the highest concentrations of flamingos are found (Talling & Talling, 1965). The concentration of flamingos generally increased as the lakes decreased in size and may

have resulted in higher TP concentrations as the season progressed. Bird exclusion experiments might help to test this hypothesis in the future. Conductivity also rapidly increased as the lakes dried out and may explain the close relationship between TP and conductivity. Although TP concentrations are highest among saline lakes with higher conductivities elsewhere in Africa, high concentrations are also found in shallow productive lakes with low salinities (Talling & Talling, 1965).

Total dissolved phosphorus was about 50% of TP in the north basin, suggesting that a large proportion of TP present there occurred in particulate form. High sediment loading in the form of silt and clay from the Nata River contributed to high turbidity. In the middle basin, TDP made up a much larger proportion of TP and increased as the lake dried out. Conditions in the middle basin were less turbid compared with the north basin. Similarly, the water in the south basin was very clear when the samples were taken as a result of less silt and clay on the sediment surface and the extensive algal mats that covered large proportions of the sediment bed in the south basin (Chapter 4) may have prevented wind-induced mixing. Concentrations of TP comprising, in some cases, 100% dissolved P indicate that whatever phosphorus exists, is available to algal growth.

NO_3^--N can be limiting to the primary production of saline lakes, particularly, in those that are eutrophic (Talling & Talling, 1965; Horne & Goldman, 1994). TN was high in all three basins, but it is impossible to say how much of this was available in the form of NO_3-N and NH_4^+ (Fig. 3.15). NO_3^--N found in the three rivers were very similar to TN in the north and middle basins during the early part of the 1999-2000 season (3.14 & 3.15), indicating a large percentage of TN loading came from the surrounding catchment and in an available form for plant uptake. TN values were highest in the north basin and increase in concentration with time, which may be owing to continued input from the inflowing rivers. Also, owing to exceptional flooding during the 1999-2000 wet season, a large population of flamingos, fish and fish-eating water birds in this lake may have contributed to large inputs of ammonium, through excretion, and rapid regeneration of nutrients from the food chain. The presence of dense blue-green algae concentrations towards the end of the 2000-2001 wet season, that often formed a 'slick' on the water

surface in calm conditions (Chapter 4), may have 'fixed' large amounts of N_2 gas from the atmosphere, and contributed to higher TN concentrations. Again experiments, using blue-green algae in cultures of low nitrogen concentrations, would help test this hypothesis. Concentrations in the middle and south basins were slightly less and decreased as the lake dried out. Shallow waters, providing more light and higher temperatures, encouraged high epipelic periphyton production and may have increased nitrogen uptake (Chapter 4). It is also likely that the top layers of the sediment were becoming increasingly anoxic, owing to the increased benthic growth, which would have provided favourable conditions for denitrification and the loss of nitrogen from the sediment as nitrogen gas.

According to Redfield (1958), a standard molar ratio for carbon, nitrogen and phosphorus (C:N:P) of 106:16:1 exists in living phytoplankton biomass. This corresponds to a similar ratio of available nutrients in seawater, of 1:15:1000 (Redfield, 1958). A N:P ratio of 16:1 may, therefore, be required in solution for phytoplankton growth. Viner (1977) later estimated this ratio to be 14:1, from the N:P ratio calculated in the blue-green phytoplankton of Lake George. According to the ratios in the three basins, phosphorus may, therefore, have been limiting to primary production in the north basin and in the middle basin at the beginning of the season (Fig. 3.16). Mean N:P ratios in the north basin were, in general, nearly double the required ratio for phytoplankton growth and were similar to the N:P ratios in two highly productive African lakes, Lake Kyoga (39) and Lake George (27) (Hecky *et al.*, 1996). The ratio decreased in the middle basin towards the end of the season to suggest nitrogen limitation. The ratio was even lower in the south basin and decreased to a minimum recorded ratio of 2.3, which suggest severe nitrogen limitations to algae production. The presence of dense concentrations of blue-green algae in the middle and north basins, particularly, in the periphyton (Chapter 4), suggests that there may be a very high turnover of nutrients in these shallow waters or the algae were 'fixing' their required nitrogen from the atmosphere. It could also be that nitrogen concentrations in the middle and south basins were underestimates owing to the very high salinities that occurred there.

3.4.5 Conclusions

There is a clear salinity gradient among the basins of Sua Pan and each basin appears to represent different stages in surface brine evolution, whereby the salinity of their waters is controlled by the variable combinations of inputs (from river runoff, saline groundwater, and the dissolution of surface efflorescence) and evaporative concentration. The proportion of input by each of the above is determined by the different hydrological regimes for each basin (Chapter 2). A large input of freshwater from the Nata River is the predominant controlling factor determining salinity and chemical composition in the north basin. Its waters are, therefore, the least saline and dominated by calcium and bicarbonate ions. Dissolution of surface efflorescence and groundwater input have, however, a much more influential role in controlling higher salinities in the middle and south basins and chemical compositions that are dominated by sodium and chloride ions. Lake water salinity also varied temporally owing to changes in the processes of flooding, at the beginning of the season, and evaporative concentration of ions and the precipitation of certain minerals out of solution, as the lakes dried out. Less saline waters at the beginning of the floods change from calcium, sodium and bicarbonate dominated waters to waters dominated by sodium and chloride ions. Large spatial and temporal variation in salinities (Fig. 3.2) contributed to a harsh and dynamic chemical background within which flora and fauna must survive and reproduce. Some plants and animals survive in certain salinities and their spatial distribution was, therefore, controlled by the different salinities of the three basins. Temporal changes in salinity also resulted in a change in community compositions over time in each basin. These ideas are explored in more detail in chapters 4 & 5.

pH was high in the waters of Sua Pan, with values ranging, generally, between 9 and 10 (Fig. 3.3). pH in all three basins increased with salinity and reached a maximum (between 9.5 and 10) above a conductivity of 20 ms cm^{-1} (Fig 3.4). The highest pH values recorded, however, occurred at the beginning of the floods in all three basins. An apparent lag period in the pH equilibrium may have resulted from large HCO_3^- inputs from the rivers and the initial dissolution of carbonates on the pan surface. High pH in the

basin waters may have influenced community composition of the flora (Chapter 4) and fauna (Chapter 5) in the waters of Sua pan.

Nutrient concentrations in Sua Pan, during the 2000-2001 season, were high and Sua pan would be considered eutrophic according to the trophic classification schemes used for temperate waters (OECD, 1982). TP concentrations increased to very high levels in the middle and south basins owing to increased concentration as the lakes dried up, and continual input and regeneration by large numbers of flamingos and other water birds. Nitrogen was also relatively abundant in the waters of the three basins. High concentrations in initial river discharges indicate the importance of immediate nitrogen loading from the catchment after a long dry season. Decreased nitrogen levels observed towards the end of the season, in the middle and south basins, suggest increased plant uptake in algae rich, shallow conditions (Chapter 4).

Chapter 4

Algae and primary production

4.1 Introduction

4.1.1 Primary producer diversity and community composition in African saline lakes

Most studies on saline lake flora in Africa have concentrated on the highly productive soda lakes of East Africa (e.g. Iltis, 1968; Iltis & Lemoalle, 1983; Hecky & Kilham, 1973; Talling *et al.*, 1973; Melack & Kilham, 1974; Melack, 1979*a*,*b*; 1981; 1988; Vareschi, 1982). In general, the lakes have low species diversity, with a dominant species occurring in high abundance. In East African lakes, this is often *Spirulina platensis*, which can survive a salinity range of 8.5-270 g l^{-1} total dissolved solids (Iltis, 1968; Melack, 1979*a*; 1988). Some shallow saline lakes have a high level of diversity due to physical and chemical heterogeneity (Hammer, 1986; Dumont, 1992). Richardson (1968) and Hecky & Kilham (1973) found alkalinity was the major factor differentiating diatom communities among saline lakes in East Africa. A few species with a wide tolerance to salinity and alkalinity, including *Nitzschia frustulum*, occurred in most of the lakes (Hecky & Kilham, 1973). Lind (1968) suggested that species composition found in over twenty small tropical lakes and dams in Kenya was determined mainly by pH, conductivity and alkalinity, supporting earlier suggestions of Beadle (1932) and Talling & Talling (1965). Periphyton communities of very shallow lakes can range from non-cohesive 'loose' associations of algae and diatoms, to dense complex algal associations in very shallow waters that are dominated by filamentous cyanobacteria and diatoms (Bauld, 1981; 1986; Dumont, 1992; Horne & Goldman, 1994). Their structural integrity involves the binding of the surface sediment and settled organic particles to form benthic 'mat' communities that consist of layers of physiologically distinctive microbial populations responding and contributing to steep vertical gradients in O_2, CO_2 and nutrients (Bauld, 1981; 1986).

Compared with the flora of the East African saline lakes, those in southern Africa have received less attention (Allanson *et al.*, 1990). Diversity among algae, other than diatoms, and cyanobacteria appears low (Hammer, 1986; Seaman *et al.*, 1991). Phytoplankton densities can, however, be high (Scott *et al.*, 1980; Harding, 1997). Hutchinson *et al.* (1932) found that algal species in small and often saline pans of South Africa differed from those in East Africa; with higher saline pans dominated mainly by cyanophytes, such as *Anabaena, Microcystis* and *Nodularia spumigena*, while the filamentous diatom *Aulacoseira* (*Melosira*) dominated the less saline lakes. In an extensive study on the diatoms from some 68 sites (pans, vleis and springs) in Namibia and the SW Kalahari region, three different types of wetland were classified by Cholnoky (1966) according to a number of indicator species. A number of species were associated with shallow saline lakes and pans with high osmotic pressure and high levels of nitrogen enrichment (the most saline being Etosha pan, Namibia), the most abundant and widespread genus being *Nitzschia.* The composition of the Makgadikgadi microflora is relatively unknown. Some aquatic macrophytes were listed by Mepham (1987) but occured in small depressions and river valleys near and between the main pans and not in the main basin lakes (Seaman *et al.*, 1991; Dumont, 1992). Biological factors also contribute to community composition and, for example, some species of diatom are associated with dense cyanobacteria blooms (Hecky & Kilham, 1973; Wetzel, 2001)

4.1.2 Community change and seasonal periodicity

Owing to large and often frequent fluctuations in lake levels coupled with large variations in nutrients, salinity, pH and alkalinity, species variation and periodicity in phytoplankton communities in and among saline lakes can be marked (e.g. Lind, 1968; Aleem & Samaan, 1969; Hecky & Kilham, 1973; Iltis, 1973*b*; 1974; Talling, 1986). Long-term changes in the hydrology of some lakes have also resulted in a complete change in species composition of their flora (Melack, 1979*a*; Vareschi, 1982). In Lake Chad, species diversity decreased from 200 taxa in the 3-4 $^{0}/_{00}$ salinity range to 40-50 taxa above 30 $^{0}/_{00}$ salinity (Iltis 1973*a*; Compere & Iltis, 1983). As salinity increased

cyanophytes and diatoms became dominant, and overall algal biomass, of particularly the dominant cyanophytes, increased (Iltis, 1973*b*). Similar successions among cyanobacteria and chlorophytes have been observed in southern African saline lakes (Ashton, 1985; Allanson *et al.*, 1990; Harding, 1997; Zohary *et al.*, 1996).

4.1.3 Primary production in saline lakes

4.1.3.1 Lake primary production

Photosynthesis, the process of primary production, occurs in the euphotic zone down to the 'compensation level', recognised as the level in the water column that receives 1 % of the surface light intensity and where photosynthetic gain of carbon equals its loss by respiration (Lampert & Sommer, 1997; Talling & Lemoalle, 1998). Maximum photosynthesis occurs at light saturation, where photosynthetically active radiation (PAR) is optimal (Talling & Lemoalle, 1998). Photosynthetic depth profiles indicate that, in shallow turbid waters, this occurs at depths of < 20 cm (e.g. Melack & Kilham, 1971; Talling *et al.*, 1973; Melack, 1979*b*; Lemoalle, 1983; Belay & Wood, 1984; Harding, 1997). Light inhibition of photosynthesis occurs above this level and may be an important factor controlling production in very shallow lakes during drying out periods (Carmouse *et al.*, 1983; Talling & Lemoalle, 1998). Through predation, a lot of the organic matter is transformed into higher trophic level organisms, while the remaining organisms die off and get recycled by decomposers. Gross primary production can be described as the overall production of organic compounds including the predation and non-predatory losses or the overall conversion of radiant energy to stored chemical energy, over time. Net primary production is the gross accumulation over time of organic matter minus the losses (Wetzel & Likens, 1991; Wetzel, 2001).

4.1.3.2 Calculating primary production

A number of methods have been devised to estimate the primary production of phytoplankton in lakes *in situ* or under laboratory conditions (Vollenweider, 1971;

Wetzel & Likens, 1991). The most widely used estimates measure the rate of O_2 production, which measures close to gross productivity, but there can be considerable differences in accuracy and sensitivity among methods (Vollenweider, 1971; Ganf & Horne, 1975). For shallow saline lakes in Africa maximum production rates have been estimated to be as high as 0.7 g C m^{-2} h^{-1} and 6.3 g C m^{-2} d^{-1} (Talling & Lemoalle, 1998). Daily productivity rates in many African saline lakes may exceed near-optimal, mid-day rates by a factor of approximately 9 (Talling, 1965; Ganf & Horne, 1975; Lemoalle, 1983; Vareschi, 1982).

There have been few estimates of periphyton net production in shallow saline lakes (Vollenweider, 1971; Talling & Lemoalle, 1998; Wetzel, 2001). One of the main problems for this work is the heterogeneous distribution of periphyton on their natural substrate surface (Vollenweider, 1971; Bootsma & Hecky, 2001). Periphyton production may, nevertheless, exceed that of phytoplankton in many saline lakes (Ganf, 1974*b*; Wetzel, 2001; Taylor, 1983; Hammer, 1986). The source of production is, however, unclear as phytoplankton that settles on the mud bottom community during sedimentation contributes to periphyton production (Ganf, 1974*b*).

4.1.3.3 Specific production rates

In general there is an inverse relationship between specific photosynthetic rates (Talling *et al.*, 1973) and population density (Ganf, 1972). High rates have, however, been associated with large chlorophyll *a* concentrations in tropical shallow saline lakes in East Africa owing to large nutrient and CO_2 or HCO_3 reserves and overall higher temperatures that increase the photosynthetic capacity of phytoplanktonic algae (Talling *et al.*, 1973; Allanson & Hart, 1975; Melack, 1979*b*; 1988; Lemoalle, 1983). Some of the highest specific production rates measured come from shallow saline lakes in Africa (e.g. Talling, 1965; Talling *et al.*, 1973; Ganf, 1974*a*; Melack, 1979*b*; Lemoalle, 1983; Belay & Wood, 1984).

4.1.3.4 Factors controlling primary production in saline lakes

Production rates are dependant upon three main contributing factors: light, temperature and nutrient availability (including CO_2), and vary according to diurnal or seasonal changes in some or all of these factors (Carmouse *et al.*, 1983; Hammer, 1986; Dumont, 1992; Talling, 1992; Talling & Lemoalle, 1998; Wetzel, 2001). Amounts of solar energy input was shown by Brylinsky & Mann (1973) to have a greater influence on phytoplankton primary production than morphological or chemical variables. High incident light, high temperatures and increased nutrient turnover drive high photosynthetic rates in the tropics (Brylinsky & Mann, 1973; Lampert & Sommer, 1997; Talling & Lemoalle, 1998). Increased light attenuation owing to self-shading in dense communities frequently reduces the total depth of the euphotic zone in shallow lakes to less than 0.5 m (Talling *et al.*, 1973; Melack & Kilham, 1974; Ganf & Horne, 1975; Melack, 1979*b*; Vareschi, 1982). Turbidity, originating from river inflow and wind-induced mixing, reduces the depth of the euphotic zone and, therefore, reduces total primary production among phytoplankton and periphyton communities (Allanson, 1980; Hart *et al.*, 1983; Dumont, 1992; Talling, 1992). Temperature is the most important factor controlling production rates among periphyton communities (Bootsma & Hecky, 2001), particularly between 20 and 30°C (Hammer, 1986; Harding, 1997; Talling & Lemoalle, 1998).

Primary productivity in African saline lakes is often limited by the availability of nutrients (Moss, 1969; Melack *et al.*, 1982; Akhurst, 1983; Grobbelaar, 1992; Bootsma & Hecky, 2001) and accounts for much of the variation in production among lakes with similar light and temperature conditions (Brylinsky & Mann, 1973; Talling & Lemoalle, 1998). In very shallow lakes, complete mixing of the entire water column facilitates increased nutrient regeneration where nutrients would otherwise be limiting, resulting in high primary productivity (Grobbelaar, 1976; Harding, 1997). Frequent mixing of the euphotic zone also reduces negative effects of surface light inhibition and dense shading by algae (Allanson & van Wyk, 1969; Kirk, 1983; Harding, 1997; Talling & Lemoalle, 1998). Carbon can also be a limiting nutrient in productive lakes. Direct use of HCO_3 as a source of carbon may increase photosynthetic potential in some saline lakes with high

alkalinities when CO_2 uptake during high productivity is limiting (Ganf, 1972; Talling *et al.*, 1973; Vareschi, 1982). Wind-induced turbulence also increases CO_2 replenishment from the atmosphere (Talling & Talling, 1965; Harding, 1997). Despite evidence of a reduction in primary productivity at high salinities (Hammer, 1986) hypo-saline shallow lakes in Africa are some of the most productive lakes in the world (Talling, 1965; Talling *et al.*, 1973; Ganf, 1974*a,b*; Melack, 1979*b*; Vareschi, 1982; Belay & Wood, 1984; Harding, 1997).

4.1.4 Aims and objectives

The algae of many shallow saline lakes in East and southern Africa support large concentrations of Lesser flamingo (Jenkin, 1957; Berry, 1972; Brown, 1975; Vareschi, 1978; Tuite, 1979; 2000; Anderson, 2000*c*). When seasonal rains fill the Makgadikgadi salt pans, tens and sometimes hundreds of thousands of Lesser flamingo feed on the algae and cyanophytes that exist in its waters (Hancock, 1990). While, in some East African lakes, details on identification and the physical and chemical parameters controlling the growth and production of the microflora exist (Vareschi, 1978; Talling *et al.*, 1978; Melack, 1979*a*; 1988; Tuite, 1979; Livingstone & Melack, 1984), an understanding of the microflora on similar Lesser flamingo habitat in southern Africa is poor. Information about the phytoplankton and periphtyon communities on Makgadikgadi is absent in the literature and little is known about the factors that control their productivity. This chapter identifies and quantifies the algae and cyanophyte species that occurred in the phytoplankton and periphyton communities of Sua pan and estimates production and abundance of primary producers in relation to physical (Chapter 2) and chemical (Chapter 3) conditions. Specific aims were to:

1. identify and enumerate the algae and cyanobacteria in the phytoplankton and periphyton;
2. identify changes in community composition and abundance with seasonal changes in flooding and related physical and chemical variables; and
3. using chlorophyll *a* specific production rates from the literature, estimate daily and seasonal phytoplankton and periphyton production in relation to changes in seasonal variables.

4.2 Materials and methods

4.2.1 Water column microflora

4.2.1.1 Phytoplankton chlorophyll a

Water samples for chlorophyll *a* analysis were taken at each basin during the 1999-2000 and 2000-2001 wet seasons. Sampling intensity was bi-weekly during the 1999-2000 season, from January to September 2000, and weekly during the 2000-2001 wet season, from November 2000 to June 2001. On each occasion, from each basin, two samples were collected in 500 ml plastic bottles, from the top 10 cm of the water column. Owing to a reduced euphotic zone as a result of high turbidity in the lakes, it was assumed that chlorophyll *a* concentrations from the top 10 cm would represent much of phytoplankton abundance. Chlorophyll *a* was determined following extraction in methanol (Standing Committee of Analyses, 1980). On returning the samples to the laboratory, 0.1 to 1 l of sample (depending on the sample turbidity) was filtered through Whatman GF/C filter paper using a vacuum pump (maintaining a vacuum below 25 cm mercury). The filter paper was placed into a centrifuge tube containing 10 ml of methanol, wrapped in tin foil and placed in storage at 4°C. Upon removal from storage, the centrifuge tube stoppers were loosened and the samples were placed in a water bath and brought to boiling (75°C) for 60 seconds. A small amount of methanol may have been lost during this process owing to evaporation. The stoppers were tightened and the methanol was allowed to cool. The filter papers were removed and the samples were then centrifuged at 3500 rpm for nine minutes. The optical equivalent chlorophyll *a* concentrations (without correction for phaeophytin) were calculated by measuring sample absorbance at 665 and 750 nm in a 1 cm cell, using a Hach DR/4000V spectrophotometer (zeroed on methanol).

Concentration was estimated by:

$$\frac{13.9 \times (Abs665nm - Abs750) \times \text{Vol. of methanol (ml)}}{\text{cell path length (cm)} \times \text{Vol. of sample filtered (litres)}}$$

A mean concentration in mg m^{-3} was calculated from the two samples taken on each occasion. It was assumed that, when using Chl *a* as an indicator of phytoplankton abundance and to base production P:B ratios on, specific concentrations were spatially and temporally constant within algal populations.

4.2.1.2 Phytoplankton sampling

Phytoplankton was sampled weekly from each basin of Sua Pan during the 1999-2000 and 2000-2001 wet seasons; from November 1999 to September 2000 and from November 2000 to June 2001. Samples were taken in a similar way to chlorophyll *a* samples; 25 ml from the top 10 cm of the water column. The depth of the water was measured at each sampling site, on each occasion. Owing to the very shallow nature of the basin lakes, boats could not be used to sample the entire area of each basin and walking was the only practical method of getting to the sampling sites. Distances between lake shores, however, often exceeded 10-15 km and it was almost impossible to sample from the whole area of each lake. An area, designated using a Magellan® GPS, that could be crossed on foot was, therefore, chosen to represent the total area of the lake in each basin (Fig. 4.1). On each occasion samples were replicated five times at random from the designated area, by dividing the selected area into numbered sections on paper and choosing which sections to sample by picking their respective numbers from a bag. Abundance and production results, later estimated from these samples, were assumed to represent the total area of each lake. The same random sampling process was carried out on the whole lake area in each basin when the lakes were small enough to do so, at the beginning and end of the flood cycles in each basin. Lugols iodine was added to the samples in the field, using a medicine dropper. Samples were then stored for further examination in the Botswana Ash (Ltd.) Pty. microbiology laboratory. One live sample (unpreserved), from each site was identified immediately on return from the field in order to account for possible deterioration of delicate species. Sampling from the middle basin

continued until the basin dried up. On occasion during the 1999-2000 season, sampling the south basin was not possible owing to its inaccessibility, particularly during extreme weather conditions and sampling ceased in May, some months before it dried up in July.

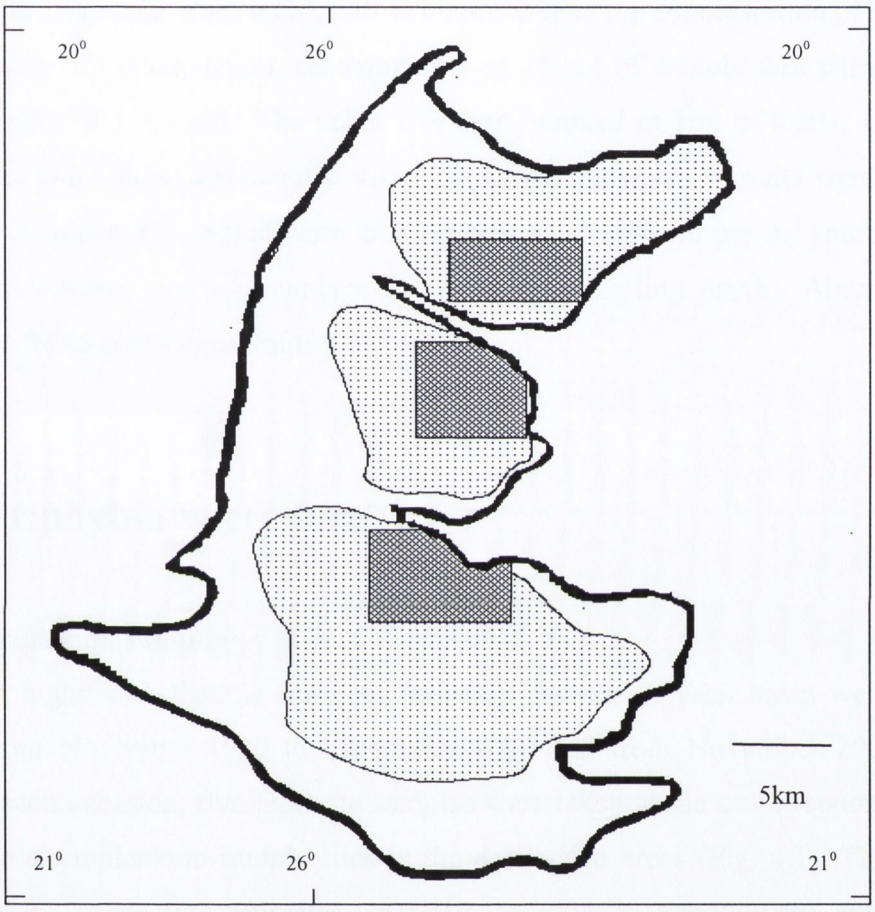


Figure 4.1 Designated areas (dark shading) of large flooding (light shading) where random samples were taken.

4.2.1.3 Identification and Enumeration

Enumeration and floral identification was carried out under a compound microscope. Sub-samples were taken from the samples with a glass pipette and placed onto a haemocytometer. Cells and filaments (colonies) were counted under x20 objective. Generally three counts were done for each sample or additional counts were carried out

until 100 individuals of the most common species were counted. Identification also took place under x60 and x100 (oil immersion) objective. Where possible phytoplankton were identified to genus using freshwater floras and some floral records from saline lakes (Cholnoky, 1966; Welsh, 1964; Hecky & Kilham, 1973; Pentecost, 1984). Owing to the very high turbidity of the lakes in each basin, counting proved extremely difficult using sedimentation methods, even with small volumes. Where the concentration of individuals was necessary for enumeration, centrifugation of 15 ml of sample was carried out for fifteen minutes at 1500 rpm. The pellet was then remixed in 1ml of water, from which sub-samples were taken and counted using the haemocytometer. Results were expressed in cells or colonies ml^{-1}, which were later express as abundance per m^3 (number ml^{-1} x 10^6) and abundance per m^2 (numbers m^{-3} / 0.1 m; sampling depth). Abundance was estimated ± 95 % confidence limits (95 % CL).

4.2.2 Periphyton microflora

4.2.2.1 Periphyton sampling

Blue-green algae and diatoms from the sediment surface of each basin were sampled weekly, from November 1999 to September 2000 and from November 2000 to June 2001. On each occasion, five replicate samples were taken at the same randomly chosen sites as the phytoplankton sample sites in the designated areas (Fig. 4.1). The resulting abundance and production estimates were also assumed to represent the entire area of each lake. Preliminary work was carried out to establish an appropriate sampling method. Glass slides and petri dishes were put down on the sediment surface in an attempt to quantify periphytes and colonization/growth rates. This technique proved to be unsuccessful owing to the large amounts of sedimentation occurring rapidly on the plate surfaces. A method using 50 mm diameter plastic tubing, proved to be the most practical way of taking consistent quantitative periphyton samples from the sediment surface. A 1m long tube was blocked at one end causing an airlock (to prevent water from the water column entering the tube) and, slowly, passed vertically through the water column to the sediment surface. By pressing the end of the tube into the surface layer of the mud

bottom 50 mm diameter plugs were isolated inside the tube. The end of the tube was then blocked and the 'plugs' were carefully removed from the sediment and brought to the surface. After removing the plugs from the tube the periphyton layer was scrapped off the surface of the plugs using a knife, and placed into a 25 ml plastic bottle. On returning the samples to the laboratory, the periphyton was re-suspended in 25 ml of water with Lugol's iodine and mixed thoroughly.

4.2.2.2 Identification and enumeration

Identification of the periphyton was carried out under a compound microscope, using the same floras as above. Owing to the nature of the sediment load and size of the blue-green algae colonies in the samples, enumeration with a haemocytometer or by sedimentation proved very difficult. Despite its inherently high variance, the 'drop transect method' (Edmondson in Vollenweider, 1971) was used as an alternative. Sub-samples from the sample were placed on a clean slide using a medicine dropper and a 22 mm cover slip placed over the drop. Drops were calibrated using a micro-syringe and sub-samples were taken to be an average of 25 µl as standard volume. The medicine dropper proved to be more effective at picking up larger algae that a micro pipette or syringe.

A stage micrometer was used to determine the width of the field of view under x20 objective. Transects across the width of the cover slip were counted and the number of cells and colonies in the total area covered by the coverslip was calculated for total transect area by:

no. cells or colonies per drop = (area coverslip/total transect area) x cells counted.

The mean number of individuals per drop was calculated for each genus. At least 100 cells/filaments of the most common species were counted from each subsample, mixing the sample thoroughly before each sub-sample was taken. The numbers of cells and colonies per sample (surface area of sample 'plug') were calculated and then converted to numbers per $m^2 \pm 95$ % CL.

After enumeration and analyses of the north basin samples, it became apparent the periphyton composition and abundance in the shallower littoral zone (defined here by the shallow areas close to the shore where benthic algae was considerably more abundant on the sediment surface when analysed) was very different to the deeper waters. The two zones were, therefore, considered separately in the analysis of average biomass and production estimates. This was important in light of the fact that 'shallow' water conditions made up a large proportion of the north lake area, particularly in the later stages of the flood period. Owing to the fact that the two zones were not sampled separately, not every sampling week included abundance results from the littoral zone, particularly in the height of the flood when it made up a small proportion of the lake surface area. Indeed, during the height of the flood, some of the weekly abundance results were calculated from just a single 'plug' sample, with the remaining random samples taken from the deep zone. Similarly, when much of the lake was shallow, abundance results for the deep zone periphyton community represent just one or two from five of the random 'plug' samples.

4.2.3 Biomass of primary producers

The biomass of the phytoplankton and periphyton community was calculated by multiplying the abundance of each species by the volume of their cells, expressed in μm^3. Cell dimensions were measured under x60 objective. The volume of filamentous colonies was calculated following Wetzel & Likens (1991) assuming colonies/filaments as 'cylinders', and total volume of filaments calculated by:

$$\pi AB^2 / 4,$$

where A is the width of the filaments and B is the total length of the filaments. Spirulina were considered coiled 'cylinders'. Diatoms were assumed cylindrical and biovolume estimated by the same equation. Biovolume of spherical cells was estimated by:

$$\pi A^3 / 6,$$

where A is the diameter of the sphere. Samples were measured weekly to monitor any change in cell volumes.

It was assumed that algae had a specific gravity of 1. Total biomass of primary producers, in μm^3 per m^3 of lake surface area for phytoplankton and μm^3 per m^2 for periphyton, was calculated on each occasion during both wet seasons. Relative contributions of each species to total biomass, was recorded as a percentage of total community biomass. Similarly, contributions made by both communities to total floral biomass were estimated.

4.2.4 Primary production

4.2.4.1 Maximum phytoplankton production rates

Maximum specific hourly production rates (P^B_{max}), expressed in mg C (mg chl *a*)$^{-1}$ h^{-1} from the literature (Table 4.1), were used to convert weekly chlorophyll *a* $\mu g\ l^{-1}$ from each basin into maximum production rates (per m^3) at light saturation. This assumed the standing crop on Sua pan contained the same photosynthetic capacity as those on the different lakes. The P^B_{max} results for each lake, taken from the literature, were expressed as a range of production, which represented the seasonal variation (Melack, 1979*b*; Belay & Wood, 1984; Harding, 1997) and the ranges occurring as a result of daily variation in weather patterns and light incidence (Talling *et al.*, 1973). Maximum specific daily rates were used (g C m^{-3} h^{-1}) and compared with those maxima calculated for all three basins. The majority of rates used were calculated using the light and dark bottle method of estimating gross primary production (Vollenweider, 1971; Wetzel & Likens, 1991). The results, given in mg O_2 (ml chl *a*)$^{-1}$ h^{-1}, were converted to mg C (ml chl *a*)$^{-1}$ h^{-1} by multiplying by the molar conversion factor of 0.375 (Wetzel & Likens, 1991), assuming a photosynthetic quotient (P.Q.) of 1.2.

4.2.4.2 Daily and seasonal phytoplankton production

Using a daily production-biomass ratio, from the literature (Harding, 1997) weekly areal chlorophyll *a* abundance, per m^2 of the top 10 cm, were converted to daily phytoplankton production in all three basins of Sua pan. A mean chlorophyll *a* specific production rate

(*P:B*) of 12.2 ± 6.7 (standard error), calculated by Harding (1997) in Lake Zeekovlei (a shallow turbid lake in South Africa) was used to calculate the integral daily rates of production, expressed in g C m^{-2} d^{-1}. Seasonal production rates were estimated by plotting the daily production values against time and measuring the area under the curve (Vollenweider, 1971; Wetzel & Likens, 1991).

Table 4.1 Maximum chlorophyll *a* specific hourly production rates (P^B_{max}) from a selection of saline lakes in Africa. Those specific rates given in mg O_2 (mg chl a)$^{-1}$ h^{-1} were converted to mg C (mg chl *a*)$^{-1}$ h^{-1} using the C : O_2 ratio 12 mg C / 32 mg O_2 = 0.375, assuming a P.Q. of 1.2 (Wetzel & Likens, 1991)..

Lake	(P^B_{max}) (mg C/mg chl *a* h^{-1})	Author
Kilotes (Ethiopia)	6.1 - 12.6	Talling *et al.*, 1973
Aranguadi (Ethiopia)	4.1 - 6.7	Talling *et al.*, 1973
Simbi (Kenya)	0.37 - 7.1	Melack, 1979*b*
Abiata (Ethiopia)	5.5	Belay & Wood, 1984
Zwei (Ethiopia)	3.6	Belay & Wood, 1984
Zeekoevlei (South Africa)	1.6 - 7.9	Harding, 1997
Hartbeespoort Dam (SA)	1.5 - 14.3	NIWR, 1985
McIlwane (Zimbabwe)	4.9 - 9.1	Robarts, 1979

4.2.4.3 Periphyton

Before the periphytic community production estimates could be calculated, algae and diatom biomass (wet weight) had to be converted into chlorophyll *a* concentration. Chlorophyll *a* varied between 0.38 and 1.31% of total phytoplankton biomass (wet weight) over the two flood periods. The regression equation: $y = 0.997x - 4.866$ (R^2 =

0.92, n = 71, all variables log transformed) was calculated by plotting the log transformations of phytoplankton wet weight against the chlorophyll *a* concentrations for each sample (Fig. 4.2) and used to convert weekly periphyton wet weight biomass estimates into chlorophyll *a* in order to calculate periphyton production using P:B ratios, based on chlorophyll *a* measurements of biomass. This calculation assumes that the chlorophyll *a* content of the different algae cells and species was constant both throughout the season and among communities.

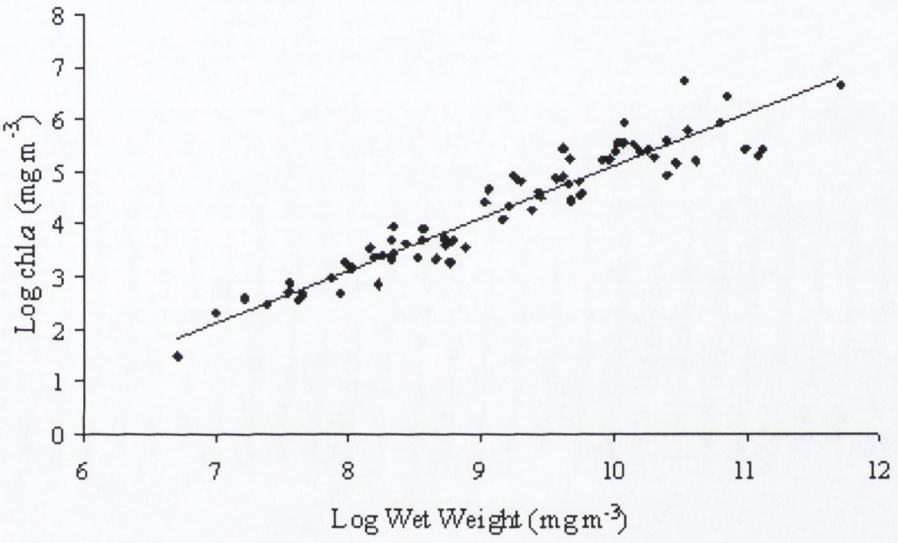


Figure 4.2 Linear regression of the chlorophyll *a* concentrations and corresponding biomass of the phytoplankton community during the 1999-2000 and 2000-2001 season (y = 0.997x – 4.866, R^2 = 0.92, n = 71, all variables log transformed).

The periphyton chlorophyll *a* estimates were then converted to seasonal production using the same chlorophyll *a* specific daily production rate (Table 4.1). The regression equation was also used to convert the biomass of the phytoplankton community on weeks when chlorophyll *a* measurements were not taken in order to provide complete seasonal production curves.

4.2.4.4 Total phytoplankton and periphyton production

The total phytoplankton and periphyton community production estimates were calculated for each basin during both the 1999-2000 and 2000-2001 seasons and summed up to give total seasonal productions for both communities during both seasons. Phytoplankton and periphyton production from all three basins were also combined to give a figure for total primary production on Sua pan during both seasons.

4.2.5 Statistical methods

The differences in phytoplankton and periphyton abundance and productivity among the three basins of Sua Pan over time was tested using Repeated Measures ANOVA (RM-ANOVA) on Data Desk® Version 6. Abundance, as wet weight biomass or chlorophyll *a*, and productivity were the dependent variable and basin and sampling date the two independent variables, with sampling date providing repeated measures on basins. Sampling date was treated as random and was nested within basins. Weekly abundance and productivity results were, however, unequal among the three basins owing to the differences in flood periods. Abundance and productivity values were log transformed in order to normalise the data before carrying out the test, with data normality investigated using normal-probability plots.

The Pearson Product-Moment correlation was used to test for associations between abundance and productivity values of phytoplankton and periphyton communities and the variables water depth, temperature, pH, total dissolved solids, total phosphorus, total dissolved phosphorus and total nitrogen. All variables were normalised by log transformation, which was tested for using frequency distribution histograms.

4.3 Results

4.3.1 Water column data

4.3.1.1 Phytoplankton chlorophyll *a* concentrations

Chlorophyll *a* concentrations of the phytoplankton community varied considerably in and among basins (Fig. 4.3), with significant differences among basins during both seasons (RM-ANOVA, $F_{1,109} = 2719.3$, $P \leq 0.0001$, dependant variables square root transformed). Concentrations were higher in the north basin compared with the middle ($P \leq 0.03$) and south ($P \leq 0.09$) basins (LSD Post Hoc tests).

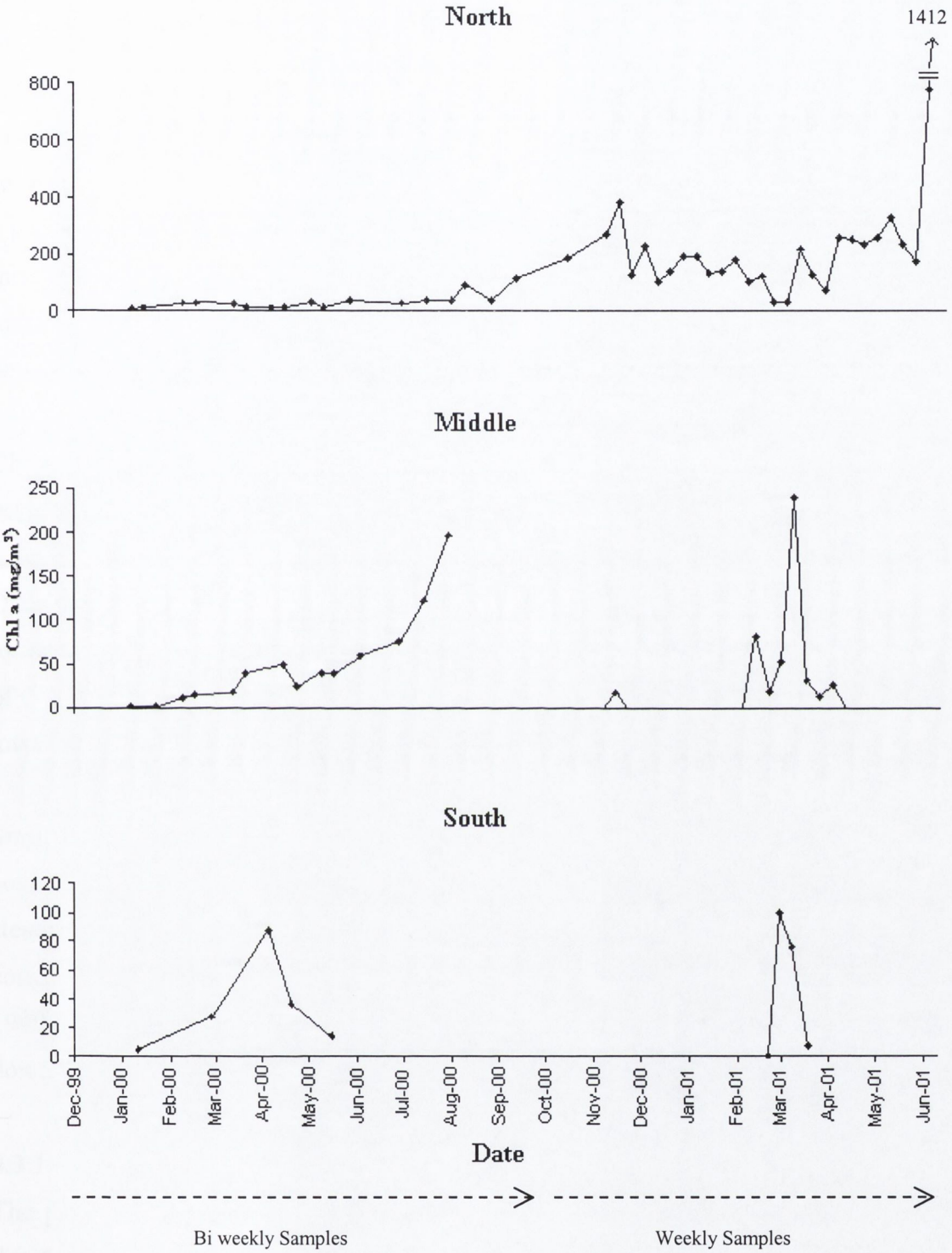


Figure 4.3 Chlorphyll *a* concentrations of the phytoplankton community in the north, middle and south basins, during the 1999-2000 and 2000-2001 wet seasons. Arrows indicate when bi-weekly and weekly sampling was carried out.

Initial (December 1999) chlorophyll *a* concentration in the north basin were low (12 μg m^{-3}). It then increased gradually to 37.9 mg m^{-3} by March 2000, after which, concentrations oscillated over the winter period of 2000. Abundance then reached a distinct peak of 379.8 mg m^{-3} in late November 2000, the beginning of the 2000-2001 season. The onset of the seasonal rains marked the decrease in concentrations again, with a seasonal low of just over 30 mg m^{-3} in late February-early March, when the majority of the season's rains fell. In late summer and early winter period of 2001 there was another increase in the concentrations, with a steep increase occurring in June. Maximum concentration recorded was 1412 mg m^{-3}.

Chlorophyll *a* concentration in the middle basin showed a similar increase over the flood period of the 1999-2000 season, from an initial low of 0.68 mg m^{-3} in December 1999 to a seasonal maximum of 196.8 mg m^{-3} in August 2000, just before the flood dried up. In December of 2000, a short flooding period saw concentrations increase rapidly from 17.8 to 221.9 mg m^{-3}, before the water quickly dried up soon after. Maximum concentrations of 240 mg m^{-3} were recorded half way through the second flood period, with fluctuating lows at the beginning and end of the flood.

Similar mid-season peaks could be identified in the patterns of chlorophyll *a* concentration in the south basin, with early season lows and concentrations decreasing steadily towards the end of the flood periods. During both seasons, chlorophyll *a* concentrations increased rapidly to peaks of 88 and 99.3 mg m^{-3} in, respectively, the 1999-2000 and 2000-2001 seasons, before rapid decreases brought concentrations back down to 14.3 mg m^{-3} in May 2000 and 7 mg m^{-3} in April 2001.

4.3.1.2 Phytoplankton composition

The phytoplankton community on Sua pan comprised relatively few algae belonging to the Cyanophyceae (cyanobacteria or Blue-green algae), Bacillariophyceae (diatoms), Chlorophyceae (green algae) and Euglenophyceae (single celled flagellate algae). The dominant genus were cyanobacteria and diatoms (Plate 4.1). The cyanobacteria included *Nodularia*, *Oscillatoria, Spirulina* and *Gleocapsa*. The diatoms included genus of

Navicula, Nitzschia, Cymbella, Epithemia and *Eunothia.* Some green algae were identified in the 'fresh' samples, but were not generally found after preservation. They included genus of *Oocystis* and a *Euglena* species.

4.3.1.3 Phytoplankton numerical abundance

Abundance of phytoplankton showed high variation in all basins, with the lowest numbers commonly occurring at the beginning of the seasons (Table 4.2). Owing to their lower abundance, *Euglena* and *Oocystis* were grouped together, as were *Cymbella, Epithemia* and *Eunothia.* A single maximum and minimum value for the north basin represents the range for the entire flood period, over both seasons. *Nodularia* and *Gleocapsa* were the most abundant phytoplankters in the north basin. *Nitzschia* was the dominant diatom genus. *Nodularia* and *Nitzchia* were dominant in the middle and south basins. *Nodularia* reached its highest population densities at the end of the flood periods, while *Nitzchia* reached peaks throughout the flood periods in each basin. *Oscillatoria* and *Spirulina* were not recorded in the phytoplankton of the middle and south basins. Less commonly occurring diatoms like *Cymbella* were also absent in the middle basin during the 2000-2001 season and completely absent in the south basin during both seasons. The numbers of *Euglena* and *Oocystis* were far lower in the middle and south basins compared with the north basin.

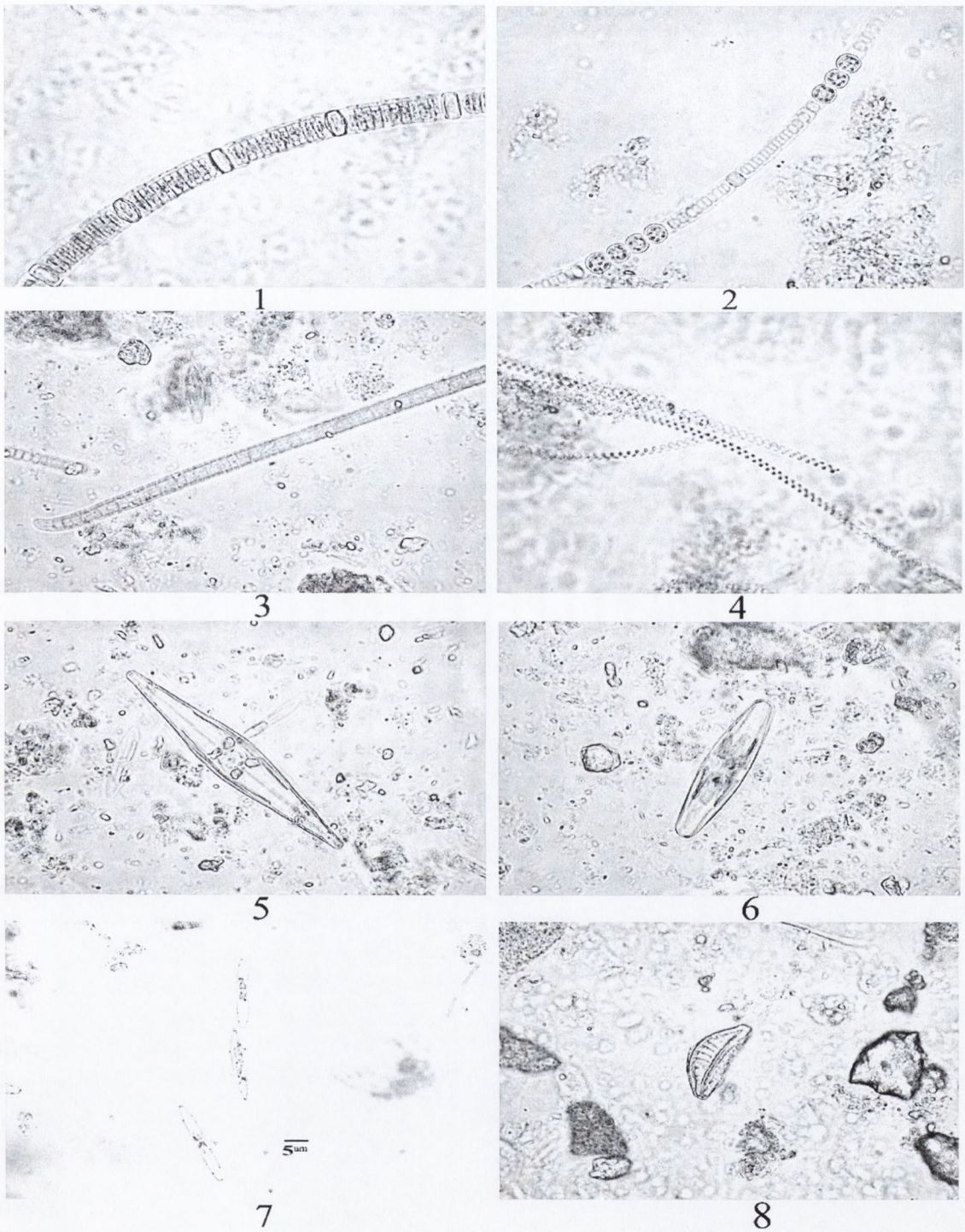


Plate 4.1 Genus of algae on Sua pan; *Nodularia* (1,2), *Oscillatoria* (3), *Spirulina* (4), *Navicula* (5,6), *Nitzschia* (7), and *Cymbella* (8). Scale bar equals 5μm and applies to all.

Table 4.2 Abundance (cells or filaments per ml ± 95 % CL) of the phytoplankton community in the north, middle and south basin lakes during the 1999-2000 and 2000-2001 season.

Algae	Season		North	Middle	South
Nodularia	'99-2000	min	0.21 ± 0.14	0.7 ± 0.2	0.8 ± 0.24
		max	-	43500 ± 4620	23300 ± 4130
	2000-2001	min	-	2050 ± 350	12.4 ± 2.2
		max	357000 ± 97300	39400 ± 4660	24900 ± 8200
Oscillatoria	1999-2000	min	0.2 ± 0.06	0	0
	2000-2001	max	59200 ± 8270	0	0
Spirulina	1999-2000	min	3530 ± 460	0	0
	2000-2001	max	111200 ± 14600	0	0
Gloeocapsa	1999-2000	min	10.5 ± 2.5	13.2 ± 1.2	36.8 ± 4.2
		max	-	229000 ± 49400	62500 ± 4500
	2000-2001	min	-	8210 ± 710	824 ± 53
		max	767000 ± 96500	1870000 ± 289460	150000 ± 17300
Navicula	1999-2000	min	0.2 ± 0.1	0.68 ± 0.22	19.8 ± 3.6
		max	-	1420 ± 260	372 ± 61
	2000-2001	min	-	17.6 ± 2.2	5.9 ± 1.3
		max	3550 ± 250	4650 ± 550	520 ± 71
Nitzchia	1999-2000	min	74 ± 12	68.1 ± 4.3	509 ± 43
		max	-	4820000 ± 894000	369000 ± 69400
	2000-2001	min	-	30100 ± 5740	269 ± 43
		max	942000 ± 87500	1950000 ± 450000	268000 ± 54000
Cymbella,	1999-2000	min	0.02 ± 00	4.5 ± 2	0
Epithemia &		max	-	565 ± 75	0
Eunotia	2000-2001	min	-	0	0
		max	3790 ± 700	0	0
Euglena &	1999-2000	min	0.6 ± 0.02	0.5 ± 0.1	0.15 ± 0.05
Oocystis		max	-	793 ± 56	779 ± 11
	2000-2001	min	-	11.5 ± 2.3	1.4 ± 0.6
		max	4880 ± 520	2210 ± 420	1.4 ± 0.6

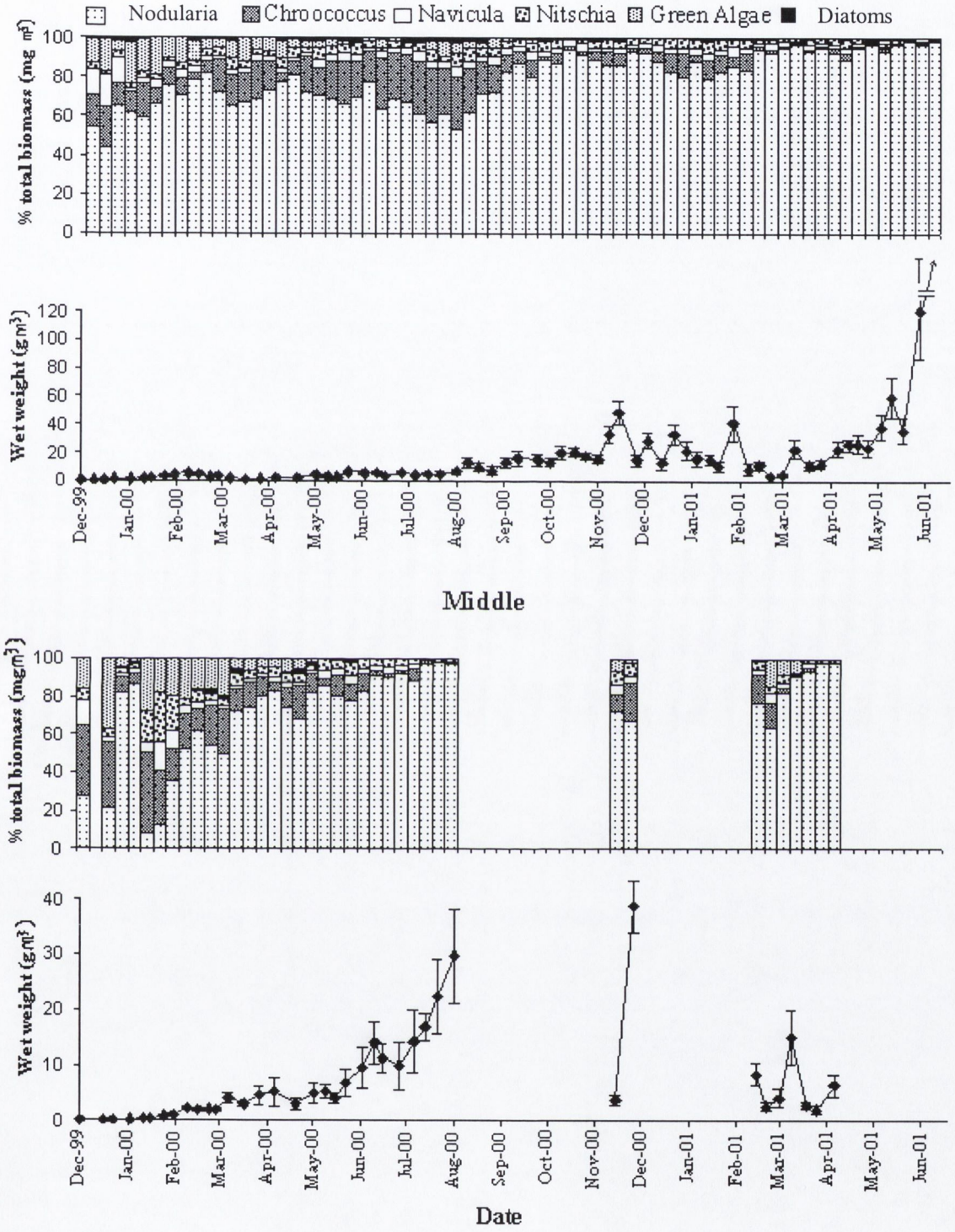
4.3.1.4 Phytoplankton biomass

The cell and filament dimensions of the algae found in phytoplankton on Sua pan varied both within and among sampling dates, which contributed to variation in relative community biomass over the two flood periods (Table 4.3). The cyanobacteria *Nodularia* and *Oscillatoria* had the largest biovolume, owing to their long filamentous structures, and dominated total community biomass.

Table 4.3 The range in cell and/or filament dimensions and biovolumes of the algae and diatoms present on Sua pan between December 1999 and June 2001.

Species	Width (μm)	Length (μm)	Depth (μm)	Biovolume (μm^3)
Nodularia	4.5 – 8			667 – 8440.3
Oscillatoria	1 – 6			32.9 – 4747.7
Spirulina	0.2 – 0.4			1.3 – 5.3
Navicula	4 – 6.5	24 – 32		301.4 – 1061.3
Nitzchia	0.8 – 1.2	2.8 – 3.4		1.4 – 3.8
Cymbella	5 – 8	18 – 22	2 – 4	180 – 704
Gleocapsa	2 – 4			4.19 – 33.5
Euglena	8	25		837.3
Oocystis	6			113

Total biomass (g m^{-3}) contributed by the different cyanophyte, and diatom genus varied within each season (Fig. 4.4).


North
Nodularia
Chroococcus
Navicula
Nitschia
Green Algae
Diatoms
% total biomass (mg m³)
Wet weight (g/m³)
Middle
% total biomass (mg/m³)
Wet weight (g/m³)
Dec-99
Jan-00
Feb-00
Mar-00
Apr-00
May-00
Jun-00
Jul-00
Aug-00
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Oct-00
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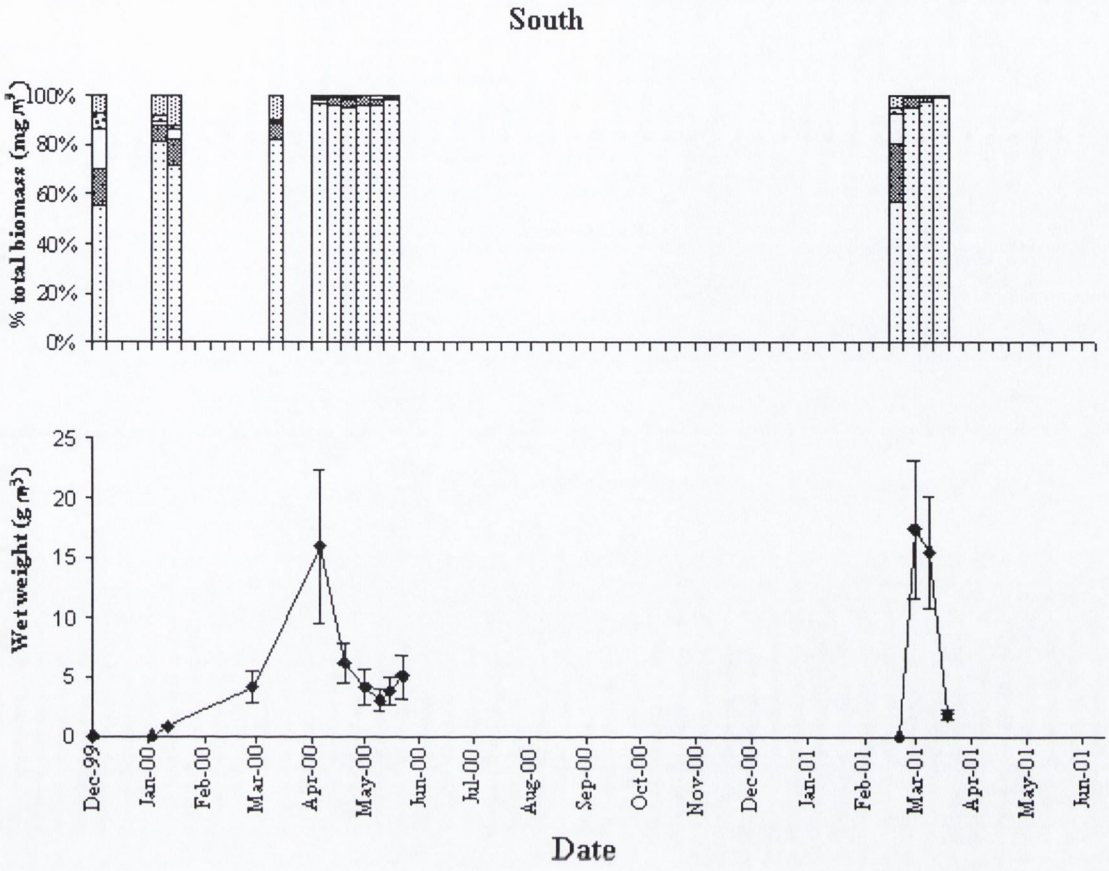

Figure 4.4 The total biomass (g m^{-3} ww) of the phytoplankton community in each basin with the percentage of the total represented by each group of algae and diatom. Error bars on biomass estimates represent 95% confidence limits.

The phytoplankton biomass of the north basin was estimated as 0.3 ± 0.12 mg m^{-3} at the beginning of the 1999-2000 season and gradually increased, with some oscillations, to approximately 15 ± 3.8 g m^{-3} by the end of the season, in October 2000. At the beginning of the season, *Navicula* and *Nitzschia* diatoms, *Gleocapsa* and *Oocystis* made up a large proportion of the total biomass. *Nodularia* quickly became the most abundant algae and dominated the total biomass during this period. During the 2000-2001 season the biomass increased, after some large early and late summer oscillations, to maximums of 120 ±

33.4 and 243.5 ± 59.7 g m^{-3} in June 2001, when sampling stopped. With the exception of some *Gleocapsa* and *Nitzchia* blooms in January and February, the total community biomass was almost completely dominated by *Nodularia*, reaching a peak of 98 % of the total biomass in June 2001.

The phytoplankton biomass in the middle basin also increased during the flooding period over the two seasons. During the 1999-2000 season the community biomass increased from 0.15 ± 0.02 g m^{-3} at the start of the season, December 1999, to 29.8 ± 5.2 g m^{-3} in August 2000, just before the basin dried up. Changes were also recorded in the contributions the various algae made to the total community biomass. The diatoms, *Euglena* and green algae, and *Gleocapsa* dominated the community during the initial flood periods, in early December 1999, and again after heavy rainfall in mid January. *Nodularia* almost completely dominated the total biomass during the latter periods of the floods in late December 1999 – early January 2000 and during the second half of that season, reaching a peak of 98% of the biomass in August 2000. The pattern was similar in the 2000-2001 season, when the basin flooded twice. The first brief flood, in early December 2000, gave rise to a phytoplankton community that quickly increased from 3.7 ± 0.92 g m^{-3} to 38.9 ± 8.5 g m^{-3} in little over a week. *Nodularia* and *Gleocapsa* dominated this community. The basin flooded again at the end of February 2001 and the phytoplankton biomass oscillated from 8.4 ± 2.1 to 2 ± 0.32 g m^{-3} at the beginning of the flood and then increased to 15 ± 3.7 g m^{-3}, before decreasing again to between 2 ± 0.46 and 6 ± 2.1 g m^{-3} before the basin dried out again. Again, at the beginning of the season, the community composition contained a lot of *Gleocapsa*, *Euglena* and *Oocystis* algae, contributing 20 to 25% of the total biomass. *Nodularia* quickly became abundant and contributed >90% of total biomass in the later half of the flood.

The abundance of the south basin phytoplankton also varied from almost a negligible community biomass of 0.001 ± 0.0004 g m^{-3}, at the beginning of the 1999 flood, increasing to 16 ± 3.6 g m^{-3} in April 2000 and declining again to 5 ± 0.9 g m^{-3}, at the end of the flood in May 2000. A similar increase and decrease in the community biomass occurred during the short flood of 2001. Abundance increased from 0.01 ± 0.002 to 17 ±

3.8 g m^{-3} and then declining to 1 ± 0.14 g m^{-3} before the basin dried out in April 2001. During the initial flood periods, the diatom *Navicula* and the cyanobacteria *Gleocapsa* were. So too, to a lesser degree, were Euglena and *Oocystis* in the early part of the large floods of the year 2000. *Nodularia*, however, dominated once again in the south basin, frequently contributing over 90% of the total biomass and reaching a peak of 98.5% at the end of the flood periods.

There were significant spatial differences in biomass over both seasons (RM-ANOVA, $F_{1,117} = 1557.6$, $P \leq 0.0001$; dependant variable was log-transformed). LSD Post Hoc tests showed that over the course of the two seasons there was significantly lower phytoplankton abundance in both the middle ($P = 0.01$) and south ($P = 0.04$) basins compared with the north basin.

4.3.2 Periphyton data

4.3.2.1 Periphyton

Aquatic macrophytes were absent on the benthos except in the north basin at the mouth of the inflowing rivers, during its prolonged flood period. The periphyton was dominated by epipelic communities of some of the same cyanobacteria and diatoms that made up the phytoplankton (Plate 4.1). The cyanobacteria *Nodularia*, *Oscillatoria, Spirulina,* and the diatoms *Navicula, Nitzschia, Cymbella, Epithemia* and *Eunothia* were identified. In very shallow waters that cover large areas of the basins, the periphyton community formed dense benthic mats that completely covered the sediment surface.

4.3.2.2 Periphyton numerical abundance

The numerical abundance of the periphyton community was, generally, higher than that of the phytoplankton (Table 4.4 and 4.5). The community of the north basin was divided into shallow (< 25 cm) and deep (> 25 cm) communities. The dominant cyanophyte *Nodularia*, for example, ranged from approximately 12 to 13000 filaments per ml in the deep areas of the north basin, to a range of 27200 to over six million filaments in the

shallow areas. In general, there was an absence of *Gleocapsa, Oocystis* and *Euglena* from the periphyton community, while the cyanophytes *Spirulina* and *Oscillatoria* were, on occasion, present in high numbers. Numbers of *Nodularia* were much lower and *Spirulina* was absent in the deep periphyton community, while *Oscillatoria* increased and became abundant as the lake got shallower. Overall abundance was generally higher in the south and lowest in the middle basin. Certain algae were, however, absent in the south basin, including *Spirulina* and the less common diatoms. *Spirulina* was also absent from the deep zone of the north basin.

Table 4.4 Numerical abundance (in cells or filaments per cm^2 ± 95 % CL) of the periphytic community in the north (deep and shallow sections) basin lake, during the 1999-2000 and 2000-2001 seasons.

Algae	Season		North Deep (>25 cm)	North Shallow (<25 cm)
Nodularia	1999-2001	min	1 ± 0.3	27200 ± 8310
		max	493 ± 96	6.53 x10^6 ± 969400
Oscillatoria	1999-2001	min	4.8 ± 1.6	29500 ± 9340
		max	264000 ± 45100	4.67 x 10^6 ± 633500
Spirulina	1999-2001	min	0	266000 ± 68200
		max	0	3.51 x 10^6 ± 563000
Navicula	1999-2001	min	326 ± 93	96500 ± 12100
		max	504000 ± 63100	1.37 x 10^6 ± 832100
Nitzchia	1999-2001	min	203000 ± 82950	661000 ± 104300
		max	9.12 x 10^6 ± 1.9 x 10^6	8.35 x 10^6 ± 2.06 x10^6
Cymbella,	1999-2001	min	309 ± 62	18000 ± 4200
Epithemia & Eunotia		max	26600 ± 8430	814000 ± 141200

Table 4.5 Numerical abundance (in cells or filaments per cm^2 ± 95 % CL) of the periphytic community in the middle and south basin lakes, during the 1999-2000 and 2000-2001 seasons.

Algae	Season		Middle (no.± 95% c.l.)	South (no.± 95% c.l.)
Nodularia	1999-2000	min	42300 ± 6930	872000 ± 130500
		max	5.26×10^6 ± 876400	7.39×10^6 ± 2.4×10^6
	2000-2001	min	75100 ± 10300	291000 ± 56700
		max	3.42×10^6 ± 626100	5.35×10^6 ± 802500
Oscillatoria	1999-2000	min	45900 ± 16340	94500 ± 11350
		max	2.55×10^6 ± 693200	325000 ± 43200
	2000-2001	min	24900 ± 8900	43800 ± 8120
		max	2.59×10^6 ± 453100	192000 ± 294500
Spirulina	1999-2000	min	174000 ± 52100	0
		max	8.4×10^6 ± 1.84×10^6	
	2000-2001	min	861000 ± 120300	0
		max	2.21×10^6 ± 456300	
Navicula	1999-2000	min	4090 ± 631	213000 ± 50620
		max	945000 ± 132500	904000 ± 232600
	2000-2001	min	4770 ± 833	102000 ± 23400
		max	128000 ± 36100	911000 ± 164400
Nitzchia	1999-2000	min	65800 ± 11260	646000 ± 88200
		max	8.2×10^6 ± 1.4×10^6	6.15×10^6 ± 843500
	2000-2001	min	338000 ± 65200	984000 ± 29300
		max	1.45×10^6 ± 192700	5.98×10^6 ± 672300
Cymbella,	1999-2000	min	18400 ± 8420	0
Epithemia &		max	780000 ± 106300	
Eunotia		min	3850 ± 681	0
		max	349000 ± 53600	

4.3.2.3 Periphyton biomass abundance

In the north basin total periphyton community biomass varied considerably with water depth (Fig. 4.5). The biomass of the shallow sections of the basin varied from 0.7 ± 0.27 g m^{-2} at the beginning of the 1999-2000 season to a maximum of 60 ± 12 g m^{-2} in June 2001. Initially *Navicula* and *Nitzschia* dominated community structure but this quickly changed to dominance by the cyanobacteria *Nodularia* and *Oscillatoria*, with *Spirulina* becoming important towards the end of the 2000-2001 season. The total biomass in the deeper parts of the basin was much lower, and ranged from 0.003 ± 0.001 g m^{-2} at the beginning of the season to a maximum of 0.3 ± 0.06 g m^{-2} by June 2001. Diatoms, particularly *Navicula*, dominated the biomass, while there were very low numbers of cyanobacteria. *Oscillatoria,* in particular, increased through the season to become an increasingly important component of the total biomass with decreasing depth of the deep areas.

The total abundance found in the middle basin (Fig. 4.6) increased from 1.2 ± 0.4 g m^{-2}, at the start of sampling, to 46 ± 16 g m^{-2} in the 1999-2000 season. In the 2000-2001 season total biomass fluctuated between 0.7 ± 0.12 to 34 ± 11 g m^{-2}. At the initial stages of 1999-2000, diatoms dominated the periphyton. Cyanobacteria then quickly became established and dominant. This dominance continued into the 2000-2001 season, with the next flood and *Spirulina* became increasingly important in the initial flood and the latter stages of the second flood of that season; although overall *Nodularia*, was, again, the dominant cyanobacteria.

This pattern of cyanobacterial dominance continued in the south basin, with *Nodularia* making up an even larger percentage of the total biomass there (Fig. 4.6). The total biomass ranged from 8.2 ± 2.4 to 58 ± 23 g m^{-2} in the 1999-2000 season and oscillated between 21 ± 6 and 35 ± 13 g m^{-2} in the 2000-2001 season, with a marked decrease in biomass during the second half of the 2001 flood period.

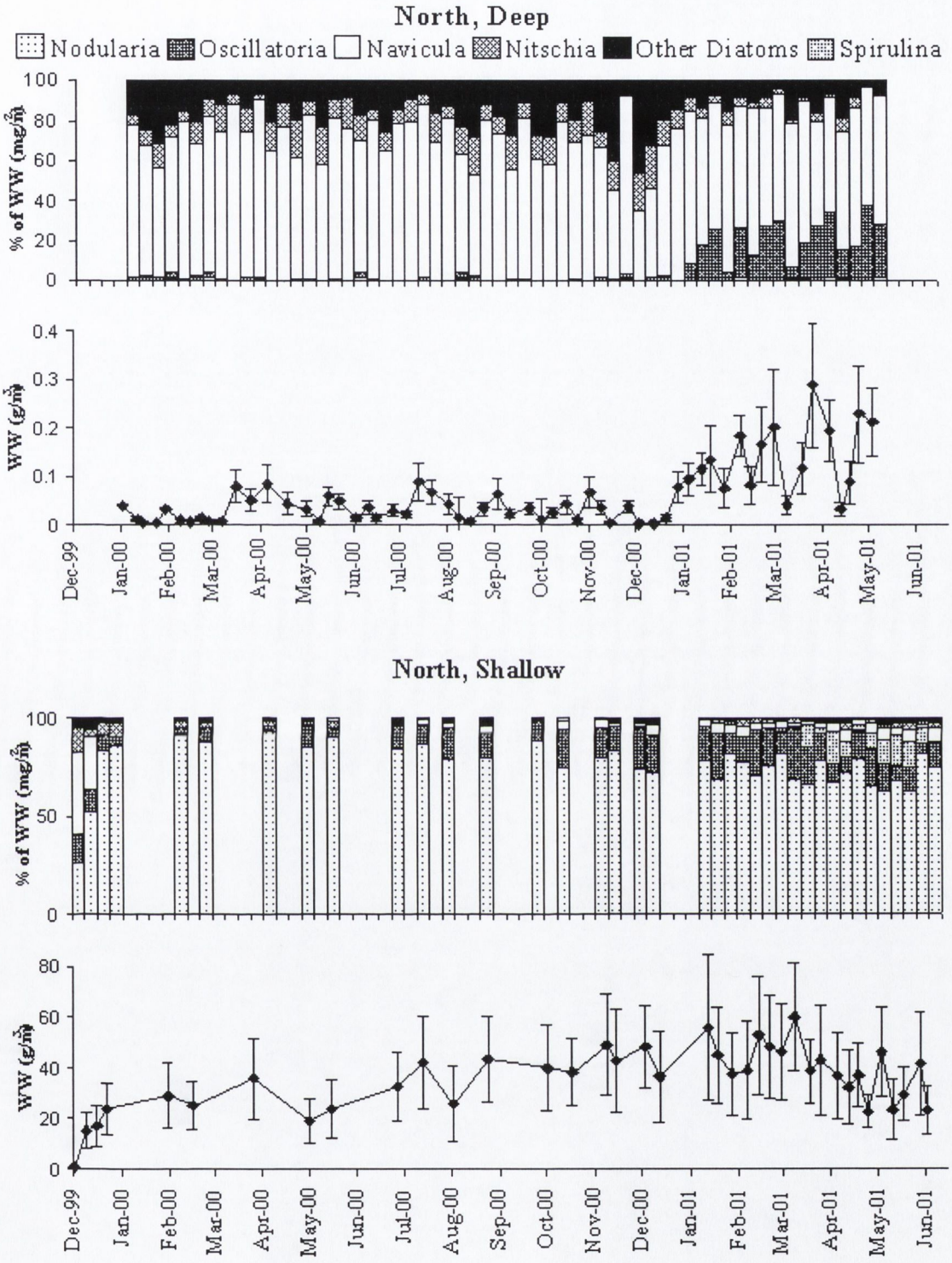

Figure 4.5 The total biomass of the shallow and deep periphyton community in the north basin, with the percentage represented by each group of algae and cyanophytes. Error bars represent 95% CL.

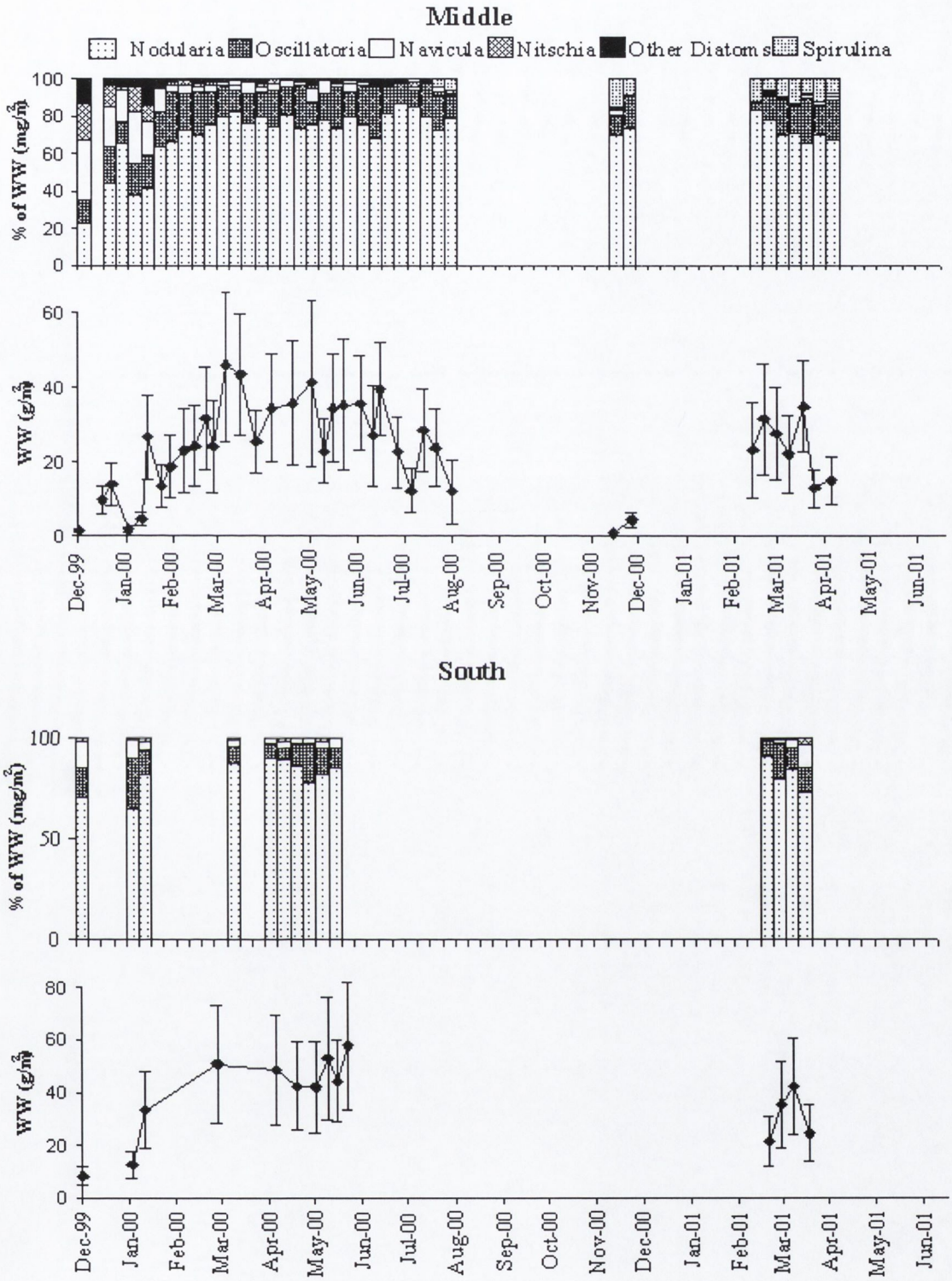

Figure 4.6 The total biomass of the periphyton community in the middle and south basins with the percentage represented by each group of algae and cyanophytes. Error bars represent 95% CL.

There were significant spatial differences in the total biomass (wet weight g m^{-2}) of the periphyton community among the three basins (RM ANOVA, $F_{1,146} = 8803.9$, $P \leq 0.0001$, dependant variables log-transformed). LSD Post Hoc tests showed that periphyton community abundance in the deep benthos of the north basin was significantly less ($P \leq 0.0001$) over both seasons compared with the shallow benthos of the north basin and the middle and south basins. The periphyton community of the middle basin was significantly less abundant than both the shallow community in the north basin ($P \leq 0.01$) and the middle basin community ($P \leq 0.04$).

4.3.2.4 Periphyton chlorophyll *a*

Assuming the periphyton community biomass comprised the same percentage of chlorophyll *a* as the phytoplankton, periphyton chlorophyll *a* concentrations were generally higher than the phytoplankton concentrations (Fig. 4.7). Chlorophyll *a* concentrations in the shallow littoral zone of the north basin varied from 5.2 mg m^{-3} at the beginning of the season to a maximum of 445.6 mg m^{-3} in March 2001. Concentrations in the deep parts of the basin were considerably lower, ranging from 0.022 to 2.2 mg m^{-3}. In the middle basin, concentrations varied between 9.2 and 343 mg m^{-3} in the 1999-2000 season and 5.45 and 260.9 mg m^{-3} in the 2000-2001 season. Concentrations were higher in the south basin, fluctuating between 61.7 and 431.2 mg m^{-3} in the 1999-2000 season and 159.4 and 264.1 mg m^{-3} in the 2000-2001 season.

There was also significant differences in concentrations among the basins during both seasons (RM-ANOVA, $F_{1,146} = 1063$, $P \leq 0.0001$, dependant variables log transformed). LSD Post Hoc tests showed that concentrations were lower in the deep north basin compared with the middle, south and shallow north ($P \leq 0.0001$). Concentrations in the shallow north basin were also significantly higher than the middle basin ($P \leq 0.01$).

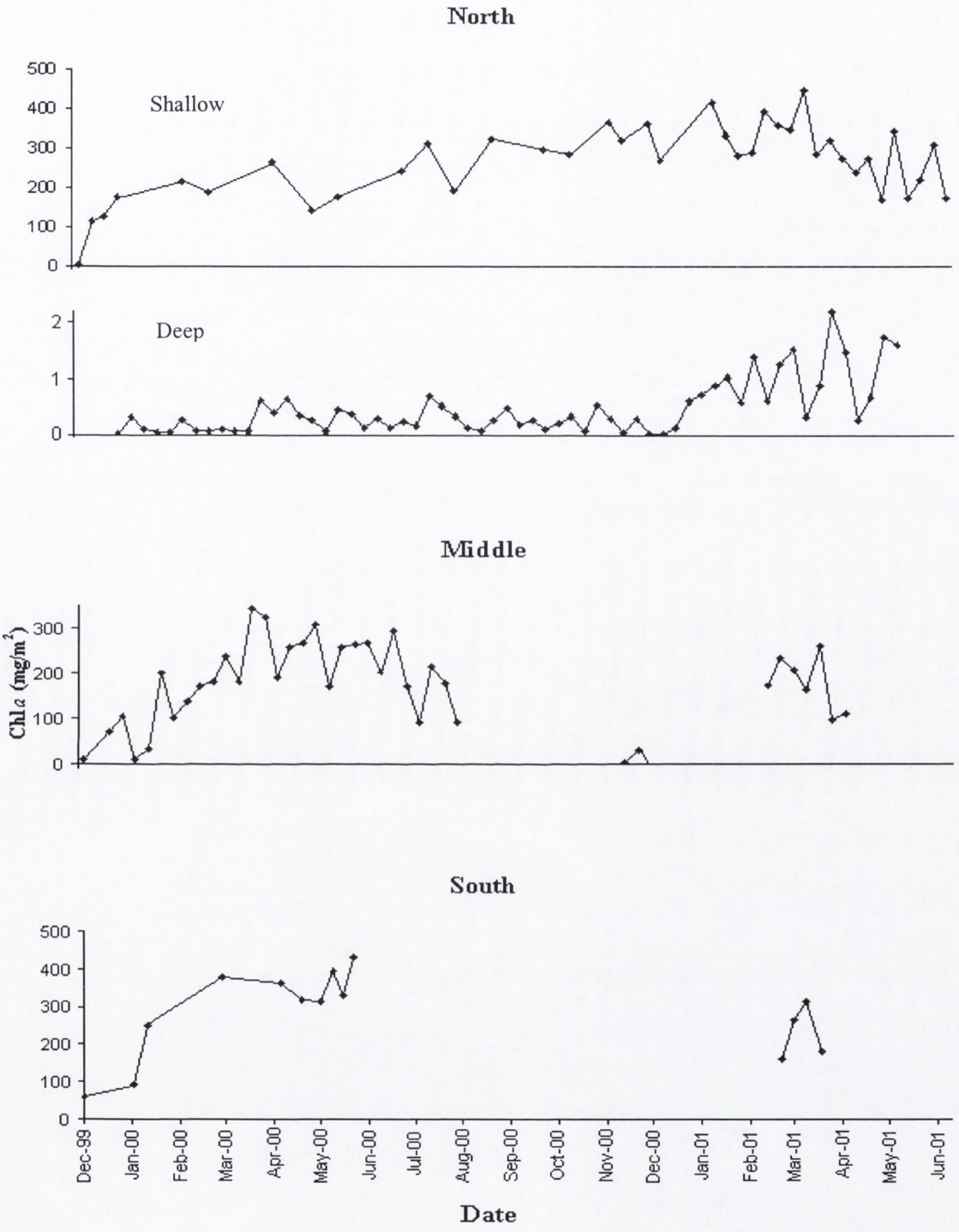

Figure 4.7 Chlorophyll *a* concentrations of the periphyton community in the north, middle and south basins during the 1999-2000 and 2000-2001 seasons.

4.3.3 Contributions to total microflora abundance

When compared with the phytoplankton community, the total periphyton community biomass in each basin was significantly different over both seasons (RM-ANOVA, $F_{1,123} = 18.3$, $P \leq 0.0001$, dependant variables log-transformed). Scheffe Post Hoc tests showed that the periphyton community was significantly more abundant than the phytoplankton community ($P \leq 0.0001$) (Fig 4.8).

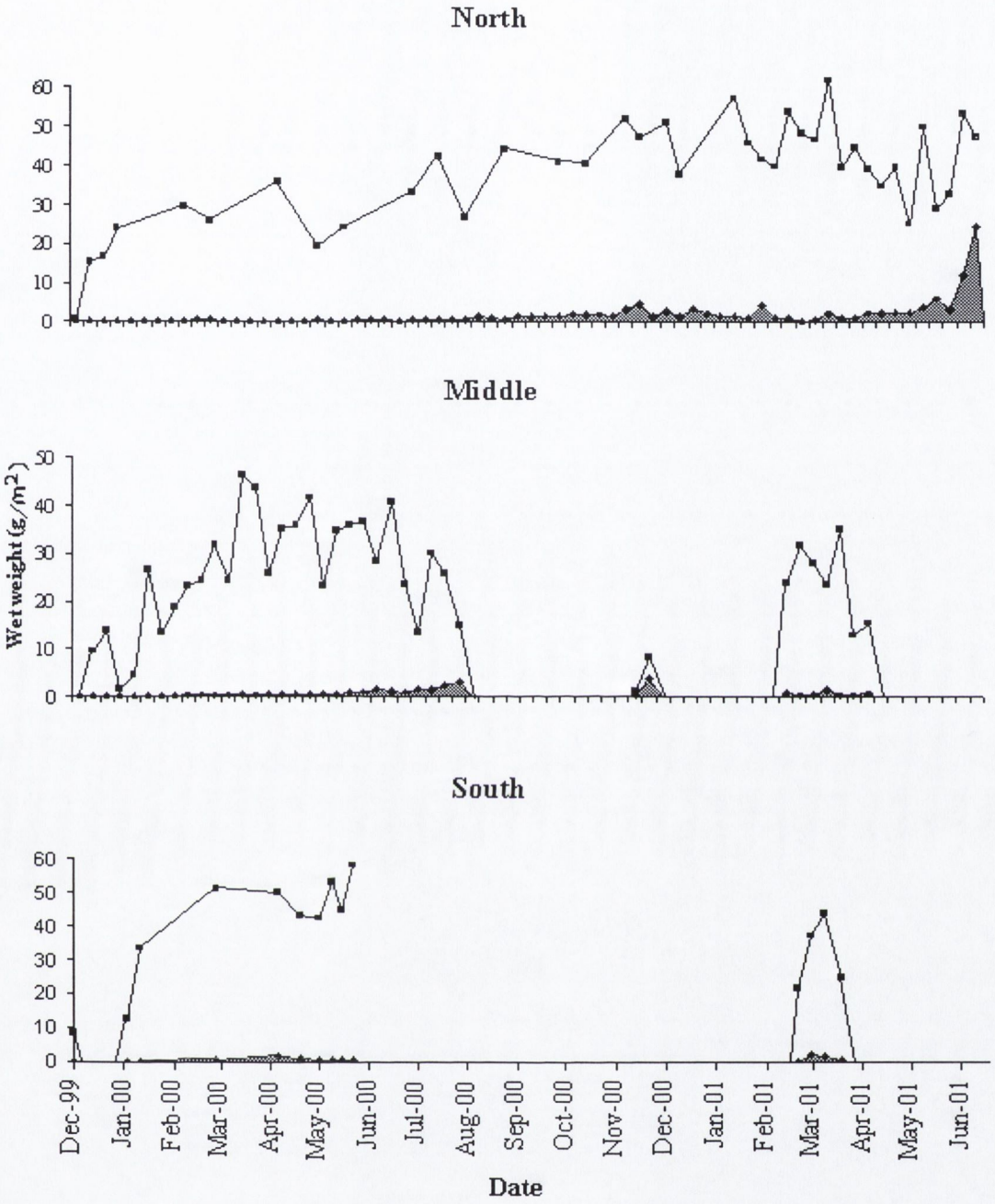

Figure 4.8 Total microflora biomass (ww) per m^2 of Sua pan, during the 1999-2000 and 2000-2001 seasons. Shaded areas represent phytoplankton biomass per m^2 of the top 10 cm of the water column; the rest are periphyton.

4.3.4 Primary production

4.3.4.1 Daily and seasonal phytoplankton production

The seasonal production curves for phytoplankton in all three basins (Fig. 4.9) represent the seasonal change in the daily integral production rate per m^{-2} of the top 10 cm of the euphotic zone, at the specific daily production rate (*P:B*) of 12.2 mg C (mg chl *a*)$^{-1}$ d^{-1} (Harding, 1997). In the north basin, mean daily phytoplankton production increased steadily from the initial floods through both seasons to the last week of sampling. Estimates remained low during the 1999-2000 season, ranging from 0.001 to 0.141 g C m^{-2} day^{-1}. A large increase in daily production rates did, however, occur in the 2000-2001 season, during which, estimates ranged from 0.105 g C m^{-2} day^{-1} to an overall estimated maximum daily production rate of 1.72 g C m^{-2} day^{-1} in June 2001. Some fluctuations did occur during this season. The most noticeable was the sharp peak at the beginning of the season and the fall in daily rates during the seasonal rains, in February. Phytoplankton mean production rates in the middle basin also increased steadily during the 1999-2000 wet season, from 0.1 mg day^{-1} to 0.24 g C m^{-2} day^{-1} by the end of the season. Similar ranges of 0.022 to 0.271 g C m^{-2} day^{-1} and 0.016 to 0.29 g C m^{-2} day^{-1} occurred during two flood periods in the 2000-2001 season. The longer second flood period, however, saw the rates gradually decrease during the second half of the flood to 0.03 g C m^{-2} day^{-1}, before the basin dried up again. In the south basin, estimates were lower, with the 1999-2000 season mean production rates ranging from 0.6 to 0.107 g C m^{-2} day^{-1} and those in the 2000-2001 season ranging from 0.1 to 0.121 g C m^{-2} day^{-1}. During both seasons a sharp increase in daily productivity at the beginning of the flood periods, was matched by a rapid decrease in rates shortly after and well before the basin dried up in the 1999-2000 season.

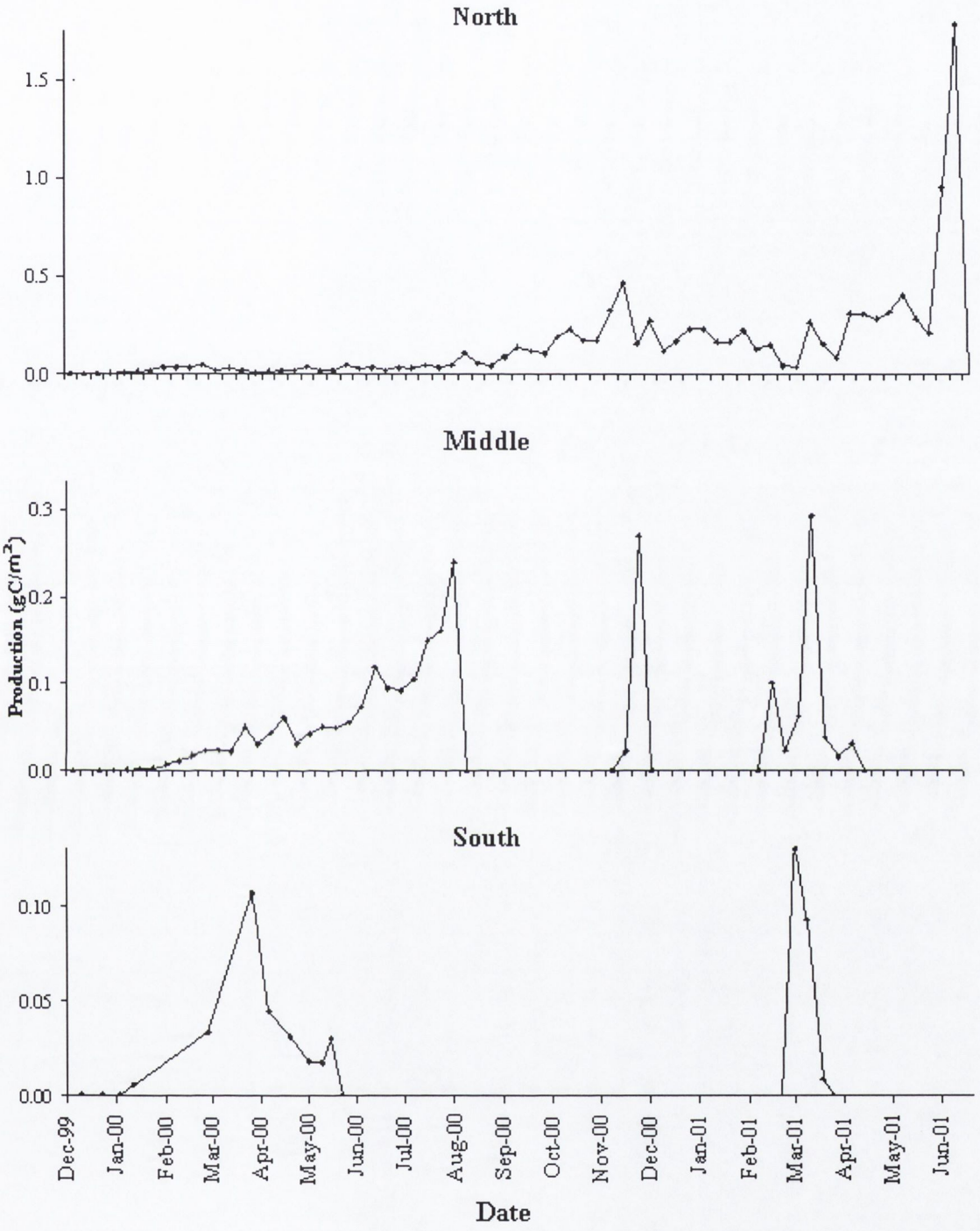

Figure 4.9 Estimated seasonal production curves for the phytoplankton community of the north, middle and south basins, during the 1999-2000 and 2000-2001 seasons.

Significant differences in phytoplankton daily rates among the basins, over the two rainy seasons, were found (RM-ANOVA, $F_{1,116} = 25.82$, $P \leq 0.0001$, dependant variables log-transformed). Subsequent LSD Post Hoc tests found that phytoplankton production in the north basin was significantly higher than that of the middle ($P \leq 0.04$) and south ($P \leq 0.01$) basins.

4.3.4.2 Periphyton production

The daily production rates of the periphyton communities were, generally higher than those of the phytoplankton (Fig. 4.10). The deep benthos of the north basin, however, had very low periphytic productivity, oscillating between 4 and 84 mg C m^{-2} day^{-1} in the 1999-2000. Production then increased from 3 to a maximum of 210 mg C m^{-2} day^{-1} toward the end of the 2000-2001 season, with large variability between weeks. In contrast, the shallow benthos of the north basin had much higher productivity, with mean daily rates ranging from 0.06 to 3.96 g C m^{-2} day^{-1} in the 1999-2000 season and 2.06 to 5.44 g C m^{-2} day^{-1} in the 2000-2001 season. A steady increase in rates occurred over the entire flood period, with a subsequent decrease in the winter months of 2001. In the middle basin production increased steadily from 0.11 to 4.18 g C m^{-2} day^{-1} during the early part of the '99-2000 season. This reached a peak at the end of March and then declined gradually during the later half of the flood period, before rapidly declining towards the end of the flood. In the 2000-2001 season a similar pattern of early increase (from 0.07 to 3.18 g C m^{-2} day^{-1}) was found during the larger flood of the season, before decreasing again before the basin dried up. Similar patterns of increase and decrease occurred in the south basin, with mean daily productivity rates ranging between 0.8 and 5.3 g C m^{-2} day^{-1} in the 1999-2000 season and between 1.9 and 3.9 g C m^{-2} day^{-1} in the 2000-2001 season.

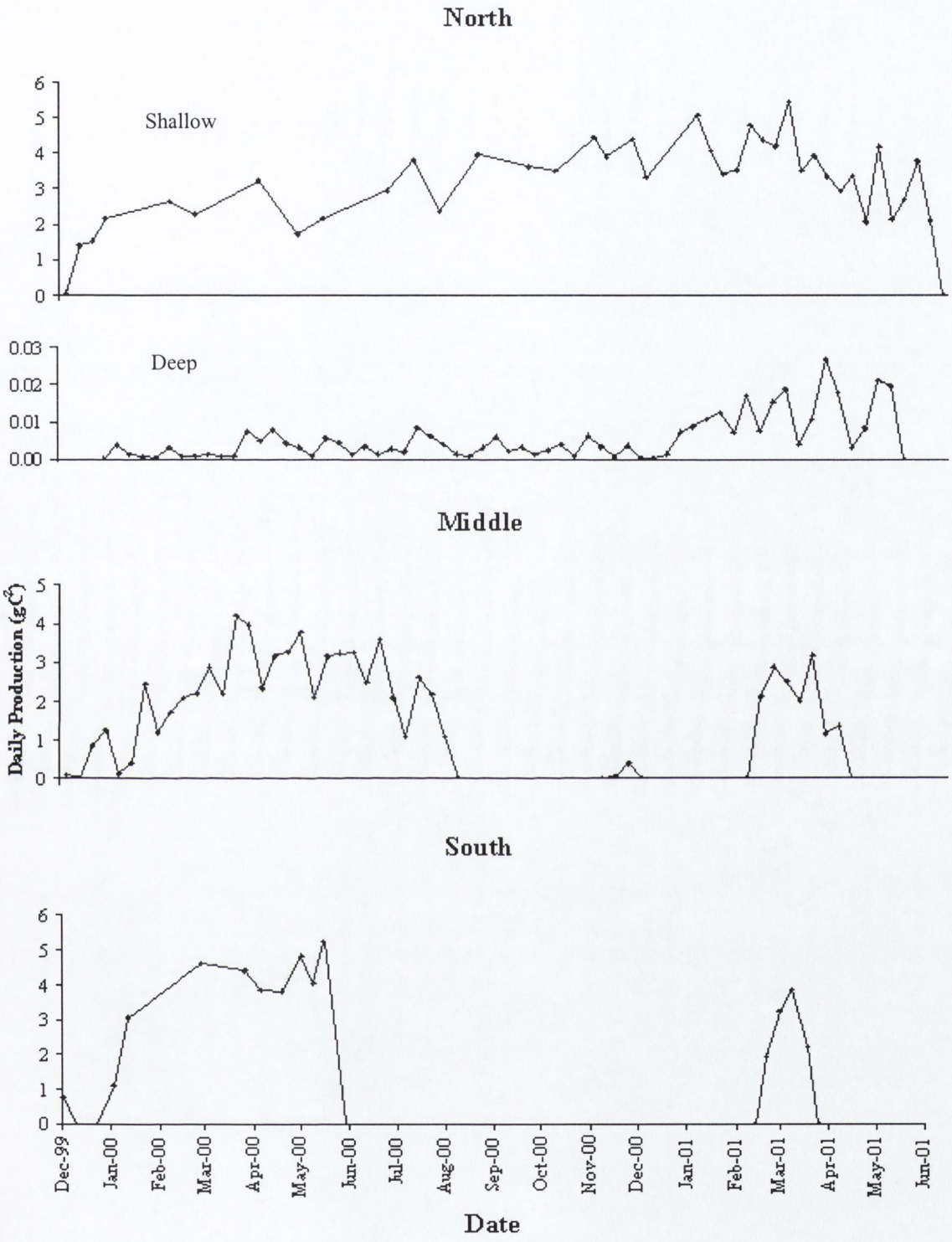

Figure 4.10 Seasonal production curves for the periphyton community of the north, middle and south basins, during the 1999-2000 and 2000-2001 seasons.

Significant differences in periphyton daily rates among the basins were also found (RM-ANOVA, $F_{1,293} = 521.59$, $P \leq 0.0001$, dependant variables log-transformed). Subsequent LSD Post Hoc tests found that periphyton production in the deep waters in the north was significantly different to the middle, south and shallow littoral zone in the north basin ($P \leq 0.0001$). Production in shallow littoral zone of the north basin was also significantly higher than that of the middle ($P \leq 0.01$) and south ($P \leq 0.04$) basins.

4.3.4.3 Contributions to total productivity

When compared with the phytoplankton community, daily production rates in the periphyton in each basin were significantly different over both seasons (RM-ANOVA, $F_{1,123} = 18.5$, $P \leq 0.0001$, dependant variables log-transformed). Scheffe Post Hoc tests showed that periphyton production was significantly higher than that of the phytoplankton community ($P \leq 0.0001$). The periphyton community contributed the majority of total primary production in each basin (Fig. 4.11).

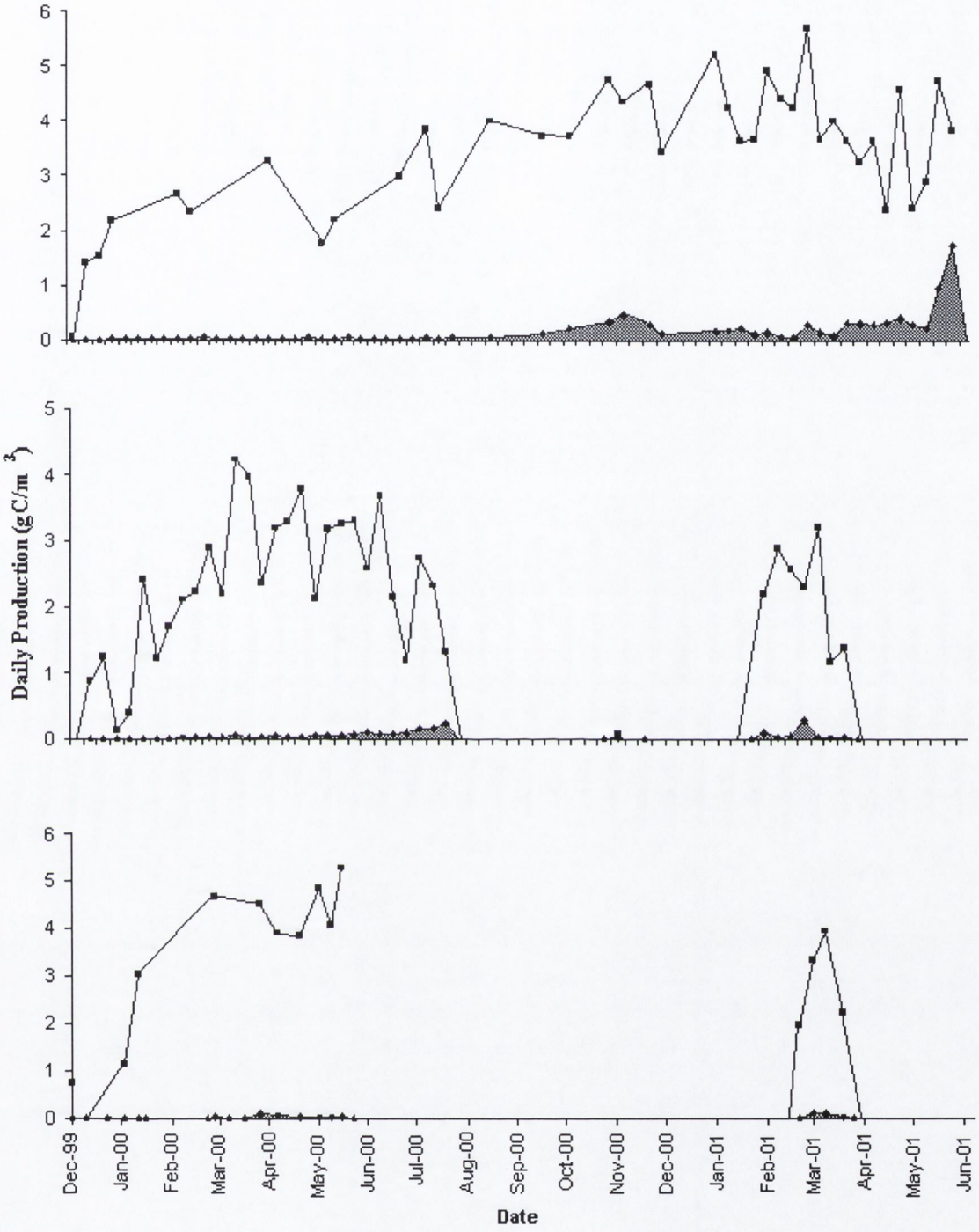

Figure 4.11 Total production of the microflora in each basin over the 1999-2000 and 2000-2001 seasons, showing the contributions of the phytoplankton (area shaded) and periphyton (area between the phytoplankton line and the top line).

Total phytoplankton and periphyton production figures for each season also shows large differences between their relative contributions to total primary production (Table 4.6). Total phytoplankton production on Sua pan was 145.7 ± 80.14 g and 684.9 ± 376.8 g for, respectively, the 1999-2000 and 2000-2001 seasons. Seasonal periphyton production on the pan was three to four times higher, totalling 607 ± 334 g and 2207 ± 1214 g for the respective seasons.

Table 4.6 The seasonal production results for the north, middle and south basin phytoplankton and periphyton communities (g m^{-2}), over the 1999-2000 and 2000-2001 seasons, using the *P:B* ratio of 12.2 ± 6.7 (s.e.) mg C (mg chl *a*)$^{-1}$ day^{-1} (Harding 1997).

Community	Basin	1999-2000 season	2000-2001 season
Phytoplankton	north	7.2 ± 3.9	64.5 ± 35.5
	middle	5.9 ± 3.2	2.9 ± 1.6
	south	1.5 ± 0.8	1.1 ± 0.6
Total		145.7 ± 80.1	684.9 ± 376.8
Periphyton	north (deep)	0.72 ± 0.4	6.49 ± 3.6
	north (shallow)	235.9 ± 129.7	2122.8 ± 1167.6
	middle	258.1 ± 141.9	61.1 ± 33.6
	south	112.4 ± 61.8	16.9 ± 9.3
Total		607.12 ± 333.8	2207.3 ± 1214.1

4.3.5 Factors controlling production

Phytoplankton showed a weak positive correlation with lake depth when the relationship between production results and depth from all three basins were tested ($r = 0.33$, n = 119, $P \leq 0.001$). The production of the periphyton, on the other hand, has a significant negative correlation with lake depth ($r = -0.54$, n = 147, $P \leq 0.001$), indicating that production decreases with depth. When correlated, there was no significant relationship between temperature and production in both the phytoplankton and periphyton communities. Salinity, however, had a significant positive correlation with the phytoplankton production of Sua ($r = 0.41$, n = 57, $P \leq 0.002$). No significant relationship was found between salinity and the periphyton community and the relationship between phytoplankton production and total nitrogen, and production and total dissolved phosphorus.

4.4 Discussion

4.4.1 Algae composition

Seasonal dry phases with preceding increases of salinity has been suggested for the complete absence of aquatic macrophytes in temporarily flooded basins (Bauld, 1986; Seaman *et al.*, 1991). Macrophytes were almost completely absence from the main pan, which has extreme lake level fluctuations and intermittent flooding. Other than those with relatively low alkalinity, an absence of macrophytes was also observed in shallow saline lakes in East Africa (Hecky & Kilham, 1973) suggesting that salinity may also inhibit macrophyte growth.

Low species richness in the phytoplankton and periphyton communities of Sua pan, is consistent with other shallow saline lakes in southern Africa (Hutchinson *et al.*, 1932; Cholnoky, 1966; Seaman *et al.*, 1991) and East Africa (e.g., Hecky & Kilham, 1973; Talling *et al.*, 1973; La Barbera & Kilham, 1974; Vareschi, 1982). Indeed, the domination of the phytoplankton by mainly one cyanobacteria species is common in shallow saline and alkaline lakes (e.g. Hutchinson *et al.*, 1932; Talling *et al.*, 1973; Iltis, 1975; Melack, 1979*b*; Vareschi, 1982). *Nodularia*, the dominant cyanophyte on Sua pan, is found in many saline lakes around southern Africa (Hutchinson *et al.*, 1932; Seaman *et al.*, 1991). The most abundant diatom species of Sua pan, *Navicula, Nitzchia* and *Cymbella* are also commonly found in similar high alkaline shallow lakes in East and southern Africa (Cholnoky, 1966; Richardson, 1968; Hecky & Kilham, 1973). The diatoms *Cymbella, Epithemia* and *Eunotia* disappeared towards the end of the flood periods suggesting their intolerance to highly saline conditions. *Oocystis, Geocapsa* and *Euglena* species also occur in numerous shallow saline lakes in East and southern Africa (summarised in; Hutchinson *et al.*, 1932; Allanson *et al.*, 1990; Lind, 1968).

The periphyton in Sua were, generally, widely distributed throughout the pan and throughout the period of flooding. This suggests an ability to tolerate wide ranges of

salinity and light, and frequent periods of desiccation (Bauld, 1981; 1986). Diatoms in the periphyton were also dominated by *Nitzschia*, *Navicula* and *Cymbella*, and similar to other shallow saline lakes in East (e.g. Hecky & Kilham, 1973; Tuite, 1981; Melack, 1988) and southern Africa (Cholnoky, 1966; Allanson *et al.*, 1990). Benthic communities comprising diatoms and cyanophytes, including *Oscillatoria* have been recorded on Lake Chilwa (Moss & Moss, 1969), but few other studies have recorded cyanophyte periphyton communities dominated by *Nodularia*. While species composition in the phytoplankton and periphyton communities were generally similar owing to the shallow nature of the water in all three basins (Hecky & Kilham, 1973; Talling, 1992), *Oocystis*, *Gleocapsa* and the *Euglena* were planktonic and *Oscillatoria* and *Spirulina* were almost entirely confined to the benthic community.

4.4.2 Spatial and temporal variation in composition and abundance

4.4.2.1 Phytoplankton

The spatial and temporal variations in the number of algae in both the phytoplankton and periphyton communities (Fig. 4.4, 4.5 & 4.6) are likely to be a result of changes in salinity and pH (Chapter 3) that occur as the lake dries up. A significant reduction in species number has been recorded on other African saline lakes that have experienced similar increases in salinity, with a few species of filamentous cyanobacteria and diatoms remaining at the highest salinities (e.g. Aleem & Samaan, 1969; Compere & Iltis, 1968; Iltis, 1974; 1975). Similarly, the phytoplankton community consisted of a higher number of algae types at the beginning of the flood periods, particularly in the north and middle basins, when *Gleocapsa*, *Euglena* and *Oocystis* and the diatoms *Cymbella, Epithemia* and *Eunothia* were present (Fig. 4.2). These genus later disappeared. Spatial change in algae diversity over time was also evident owing to different ranges in salinity among the three basins (Chapter 3). The south basin, for example, quickly developed a very simple phytoplankton community, concurrent with the rapid increase in salinities during both seasons.

4.4.2.2 Periphyton

Temporal and spatial changes in periphyton diversity (Fig. 4.5 & 4.6) also followed increases in pH and salinity. Again, fewer species were found in the south basin with the absence of the diatoms, *Cymbella*, *Epithemia* and *Eunothia*. They disappeared in the middle basin towards the end of the 1999-2000 wet season and were absent during the 2000-2001 season. Temporal variation in richness was particularly evident with the colonisation of the very shallow littoral benthos by *Spirulina* in the north and middle basins, late in the flood periods. Owing to a tolerance of high alkalinities and pH (Lind, 1968), *Spirulina* was the dominant cyanophyte genus in the alkaline rich soda lakes of East Africa (e.g. Melack, 1979*b*; Vareschi, 1982). Its absence in the south basin suggests salinities there exceeded its tolerance, although *Spirulina* exists at higher pH and salinity concentrations in some East African soda lakes (Iltis, 1973*a*; Melack, 1979*b*; 1988; Vareschi, 1982).

Variations were also heavily influenced by lake depth, particularly, in the north basin. The greatest change in community composition occurs between the deep and littoral zones of the north basin owing to the difference in light incidence to the benthos. A change from deep to shallow benthic habitat appeared to occur between 25 and 35 cm. At this depth enough light was penetrating the overlying water column to enable *Oscillatoria* and small numbers of *Nodularia* to exist with an otherwise diatom dominant community. The early colonisation by *Oscillatoria* of the deeper benthos of the north basin, as it became shallower, indicated a tolerance to low light conditions by this cyanophyte. As the lake got shallower thick benthic mats comprising dense associations of cyanobacteria, dominated by *Nodualria*, and diatoms, dominated by *Navicula* and *Nitzschia*, colonised the surface.

4.4.2.3 General flora abundance and spatial distribution

The general differences in the community structure, abundance and spatial distribution of Sua pans aquatic flora is summarised in four aerial views of the pan taken from NASAs Terra satellite, at different times during the 1999-2000 flood period (Plate 4.2). Differences in the floral abundance (the green areas of the lakes) among the basins and within each basin during the lifespan of the flood period are clearly visible and the spatial and temporal variations among the basins are evident. On the 8th of April 2000, when the basins were already receding after peak floods (Plate 4.2), the deepest northern basin appeared pale and turbid owing to large inputs of organic and inorganic material from river discharge (Chapter 2) and pan surface. Poor light incidence restricted phytoplankton growth to a shallow euphotic layer that was continually mixed in the water column by wind and rains and prevented light penetration to the majority of the lake bottom, preventing periphyton growth. Only the shallow littoral zones around the shore, particularly along the very shallow western shore, therefore, appeared green indicating high periphyton abundance. The middle and south basins, in contrast, look very different. Shallower waters coupled with higher salinities and nutrient concentrations (Chapter 3), resulted in higher floral abundance at this stage of the flood. Large areas of the middle basin and almost the entire south basin appeared green (Plate 4.2) indicating high phytoplankton abundance in the water column and dense periphytic communities covering large areas of the sediment bottom. The images taken on 24th of June and 11th of August 2000 both show different stages of drying, particularly on the middle and south basins (Plate 4.2), with periphytic growth receding with the receding western shore line and phytoplankton abundance decreasing as periphyton colonisation of the sediment surface in the east increased. On the 2nd of February 2001, just prior to following seasons rains, the last remaining water in the north basin appeared green (Fig. 4.12). Continual drying resulted in the disappearance of both the middle and south basins and reduced the north basin to a very shallow lake and conditions favourable for a dramatic increase in phytoplankton and periphyton abundance.

April 8th, 2000

July 24th, 2000

August 11th, 2000

February 2nd, 2001

Plate 4.2 MODIS satellite images of the Sua pan, taken from the Terra satellite (NASA), showing the general variation in the community type, distribution and abundance of the primary producers (the green areas) among the three basins of Sua pan.

4.4.3 Phytoplankton abundance

Maximum phytoplankton abundance in terms of cell and filament numbers, in all three basins (Table 4.2), were higher than counts made in other highly productive saline lakes elsewhere in Africa (e.g. Melack & Kilham, 1974; Hart & Hart, 1977). In general, very shallow euphotic zones, particularly at the beginning of the flood periods, combined with condensed water columns during the latter stages of the flood periods contributed to higher numbers in the top layers of the euphotic zone. Maximum counts of the dominant cyanobacteria *Nodularia* in the north basin (360000 ± 97300 filaments) exceeded counts of the much smaller *Spirulina platensis* during peak numbers of the species in the soda lake Simbi (maximum of 200000 coils ml^{-1}) (Melack, 1979*b*). This is surprising because one would expect *Spirulina*, being smaller than *Nodularia*, to occur in higher numbers in the euphotic zone before self-shading would inhibit productivity (Talling & Lemoalle, 1998). Although the diatoms *Nitzschia* and *Navicula* were by far the most abundant algae they contributed only a small fraction of the phytoplankton biomass.

Wet weight carbon or chlorophyll *a* based phytoplankton abundance varies in saline lakes according to lake depth (e.g. Grobbelaar, 1985; Allanson *et al.*, 1990), depth of the euphotic zone (e.g. Hart *et al.*, 1983; Vareschi, 1982), temperature and seasonality (e.g. Talling *et al.*, 1973; Lemoalle, 1983), nutrient availability (e.g. Moss, 1969; Akhurst, 1983), wind induced mixing of the euphotic zone or entire water column (e.g. Stegmann, 1982; Harding, 1997), and grazing (e.g. Vareschi, 1978; Moriarty *et al.*, 1973). In Sua pan, shallow euphotic zones with high temperatures (>25°C) and high nutrient levels (Chapter 3) resulted in high chlorophyll *a* concentrations that, generally, fluctuated between estimates, based on the upper 10 cm of the water column, of 20 and 200 mg m^{-3} in all three basins during both wet seasons (Fig. 4.3). These figures are similar to some of the highest concentrations found in other highly productive saline lakes in Africa (e.g. Talling *et al.*, 1973; Melack & Kilham, 1974; Ganf, 1974*b*; Melack, 1979*b*; Vareschi, 1982; Belay & Wood, 1984; Harding, 1997). Fluctuations in weekly estimates of both biomass and chlorophyll *a* concentrations, particularly in the north basin, were probably

caused by wind induced mixing of phytoplankton, which reduced concentrations in the top 10 cm (Stegmann, 1982; Harding, 1997). Turbidity fluctuations during the wet season also had a large influence on phytoplankton concentrations in the top 10 cm. Vareschi (1982) found extremely high phytoplankton abundance (1160 mg chl a m^{-3}) during a dense *Spirulina* bloom on Lake Nakuru, when the euphotic zone was at its shallowest (Secchi disc 10 cm). This changed dramatically (164 mg chl *a* m^{-3}) with an increase in the Secchi disc depth to between 40 and 50 cm. Similar fluctuations in the abundance of the phytoplankton occurred with changes in the turbidity as a result of rainfall, river discharge and wind induced turbulence (Vareschi, 1982).

The influence of lake depth on abundance is evident in the middle and south basins and in the north basin at the end of the 2000-2001 wet season. Phytoplankton density, generally, increased as lakes depth decreased below 40 cm. The reduction of the water column coupled with a decrease in the depth of the euphotic zone increases the concentration of phytoplankton in the top 10 cm (Vareschi, 1982; Dumont, 1992). Phytoplankton abundance (Fig. 4.3 & 4.4) close to the end of both flood periods in the middle basin (200 & 240 mg chl *a* m^{-3}) and south basin (90 & 100 mg chl a m^{-3}), are among the highest recorded anywhere in Africa. Estimates were higher in the north basin when it receded and decreased in depth during the 2000-2001 season (Fig. 4.3 & 4.4). Maximum abundance (780 to 1412 mg chl *a* m^{-3}) exceeded concentrations recorded from two of the most productive lakes in Africa; Lake Simbi in Kenya: 980 mg chl *a* m^{-3} (Melack, 1979*b*) and Lake Nakuru: 1160 mg chl *a* m^{-3} (Vareschi, 1982). These peaks in abundance on the north basin were associated with calm conditions and a phytoplankton dominated by *Nodularia* (>97 % of total biomass), which formed a thick green 'scum' close to and on the surface of the shallow water. Both phosphorus: 320 µg l^{-1} (of which 50 % was total dissolved phosphorus) and total nitrogen: 6 mg l^{-1} had increased to maximum concentrations (Chapter 3) and light and temperature (26°C) was high. Frequent wind induced mixing of the entire water column ensured recycling of nutrients into the euphotic zone (Talling *et al.*, 1973; Melack & Kilham, 1974; Harding, 1997).

The distinctive decreases in phytoplankton abundance in the middle and south basin at the end of the floods (Fig 4.3 & 4.4), occurred concurrently with decreased depth (<20 cm) and turbidity. The decrease in turbidity in very shallow conditions occurs as a result of an increase in the periphyton community, which gradually 'traps' organic and inorganic material settling out of the water column (Bauld, 1986; Dumont, 1992). Despite wind-induced turbulence, therefore, the water column remained clear. Increases in salinities and pH to maximum levels accompany reductions in phytoplankton abundance (e.g. Iltis, 1973*b*). Although the diatoms *Navicula* and *Nitzschia* and the cyanobacteria *Nodularia* have been recorded in waters of higher salinities compared with those in the middle and south basins during the late stages of flooding (Hutchinson *et al.*, 1932; Cholnoky, 1966; Hecky & Kilham, 1973; Hammer, 1986), dramatic increases in salinity were concurrent in Sua with dramatic decreases in phytoplankton abundance.

Grazing by, respectively, fish and invertebrates and Lesser flamingos accounted for, respectively, up to 30 % and 90 % of daily primary production in Lake Nakuru, East Africa (Moriarty *et al.*, 1973; Vareschi, 1978; Livingstone & Melack, 1984). Rapid recycling of nutrients as a result is also thought to enhance phytoplankton production, which in turn enhances feeding conditions. Abundance among and within the basins may, therefore, have been influenced by fluctuating grazing pressure by both invertebrates (Chapter 5) and Lesser flamingos (Chapter 6). This is an important aspect of ecosystem functioning, involving key top-down factors that controls the primary trophic level. Experimental on the effects of excluding predators from areas of the lake would help test the effects of predation pressure on primary community composition and productivity.

4.4.4 Periphyton abundance

Lake depth and turbidity were the primary physical factors controlling the abundance of periphyton algae and cyanobacteria on Sua pan owing to their control of light penetration to the sediment surface. The contrast of biomass estimates between the littoral and deep zones of the north basin highlights this (Fig. 4.5). The numerical aerial abundance of the

periphytic community (per cm^2) exceeds the phytoplankton counts by some orders of magnitude (Table 4.3) owing to dense mats, particularly in very shallow conditions on the south basin and at the end of the flood periods in all three basins. Cell counts for the most abundant diatoms, for example, far exceeded similar counts (1-60 x 10^4 cells cm^{-2}) from a productive benthic diatom community on the sediment of a shallow saline lake in South Africa (Bowen, 1978).

Although the majority of the phytoplankton abundance occurs in the upper layers of the water column in highly turbid lakes (e.g. Talling *et al.*, 1973; Ganf & Horne, 1975; Melack, 1979*b*; Vareschi, 1982; Harding, 1997) the much greater areal abundance (m^2) of periphyton (Fig. 4.8) is somewhat misleading owing to phytoplankton areal abundance only accounting for the top 10 cm and not the entire water column. In deeper waters this could be an underestimate, particularly when wind-induced turbulence circulates the phytoplankton throughout much of the entire water column (Harding, 1997). Nonetheless, the overwhelming dominance of the periphyton community in the total abundance of saline lake flora is far greater than abundance comparisons carried out in other very shallow African lakes, where large areas of their sediment surface are colonised by periphyton algae (e.g. Bowen, 1978; Taylor, 1983).

Grazing of the benthic mats by hundreds of thousands of Lesser flamingos (Chapter 6) may also contributed to the variance in the periphyton abundance (Fig. 4.5 & 4.6) and again simple flamingo exclusion experiments would help test this hypothesis. The impact of flamingo grazing on abundance would have been at its greatest when the birds were concentrated at the beginning of the flood periods, along the shallow shoreline and as the lakes were drying up when dense feeding flocks covered the entire area of the remaining lakes.

4.4.5 Production

4.4.5.1 Maximum production rates

Maximum photosynthetic rates estimated on Sua pan (Table 4.7) are considerably higher than some of the most productive shallow lakes in both southern and East Africa. Owing to similar chlorophyll *a* concentrations, maximum estimates in the middle and south basins were similar to production rates from Zeekovlei, Hartbeesport Dam and Lake McIlwaine in southern Africa. The north basin maximum was similar to Lake Simbi, one of the most productive lake systems in Africa. The difference in photosynthetic rates between *Spirulina* blooms on Simbi and *Nodularia* on the north basin would, however, result in different production rates. Furthermore, the likelihood of higher biomass related attenuation and resulting selfshading in the dense *Nodularia* blooms of the north basin could reduce their photosynthetic capacity (Talling & Lemoalle, 1998). Water temperatures on the north basin (18-20°C), when maximum rates occurred, were considerably lower than those recorded on the East African lakes (e.g. Talling *et al.*, 1973; Melack, 1979*b*). Temperature reductions result in reduced photosynthetic capacities (eg. Lemoalle, 1983) and, assuming production increases with temperature above 20°C, maximum productivity rates on the middle basin in August 2000 and on the north basin in June 2001 may have been lower. Similarly, maximum production rates in the middle and south basins, which compared with those from lakes elsewhere in southern Africa assume similar temperatures. Nonetheless, these comparisons indicate that maximum production rates on Sua pan are some of the highest among Africa lakes (summarised in Livingstone & Melack, 1984; Hammer, 1986; Allanson *et al.*, 1990; Harding, 1997).

Table 4.7 Maximum production rates (P_{max}) in g C m^3 h^{-1} for each basin of Sua pan compared with the maximum rates from the respective African lakes.

Lake	P_{max}	North	Middle	South
Kilotes	10135	17792	3025	1251
Aranguadi	29729	9461	1609	665
Simbi	12900	10026	1705	705
Abiata	3600	7767	1321	546
Zwei	3300	5084	864	357
Zeekovlei	1524	11156	1897	784
Hartbeesport	5916	20475	3481	1439
McIlwane	653	12850	2185	903

Daily production estimates for the phytoplankton community of the three basins (Fig. 4.11) are also similar to some of the highest rates recorded elsewhere in Africa (e.g. Talling, 1965; Melack & Kilham, 1974; Melack, 1979*b*; Talling *et al.*, 1973; Belay & Wood, 1984; Harding, 1997). These daily rates could be underestimates during maximum standing crop biomass, particularly in the north basin, where maximum production rates (Table 4.6) are much higher than at Zeekovlei (Harding, 1997).

4.4.5.2 Factors controlling primary production

High daily production rates can be attributed to a number of different physical and chemical factors that contribute to a high incidence light over long photoperiods (>10 hours), associated with high water temperatures and rapid nutrient recycling (Fig. 4.12). These factors also contribute to the high spatial and temporal variation in production and among the basins.

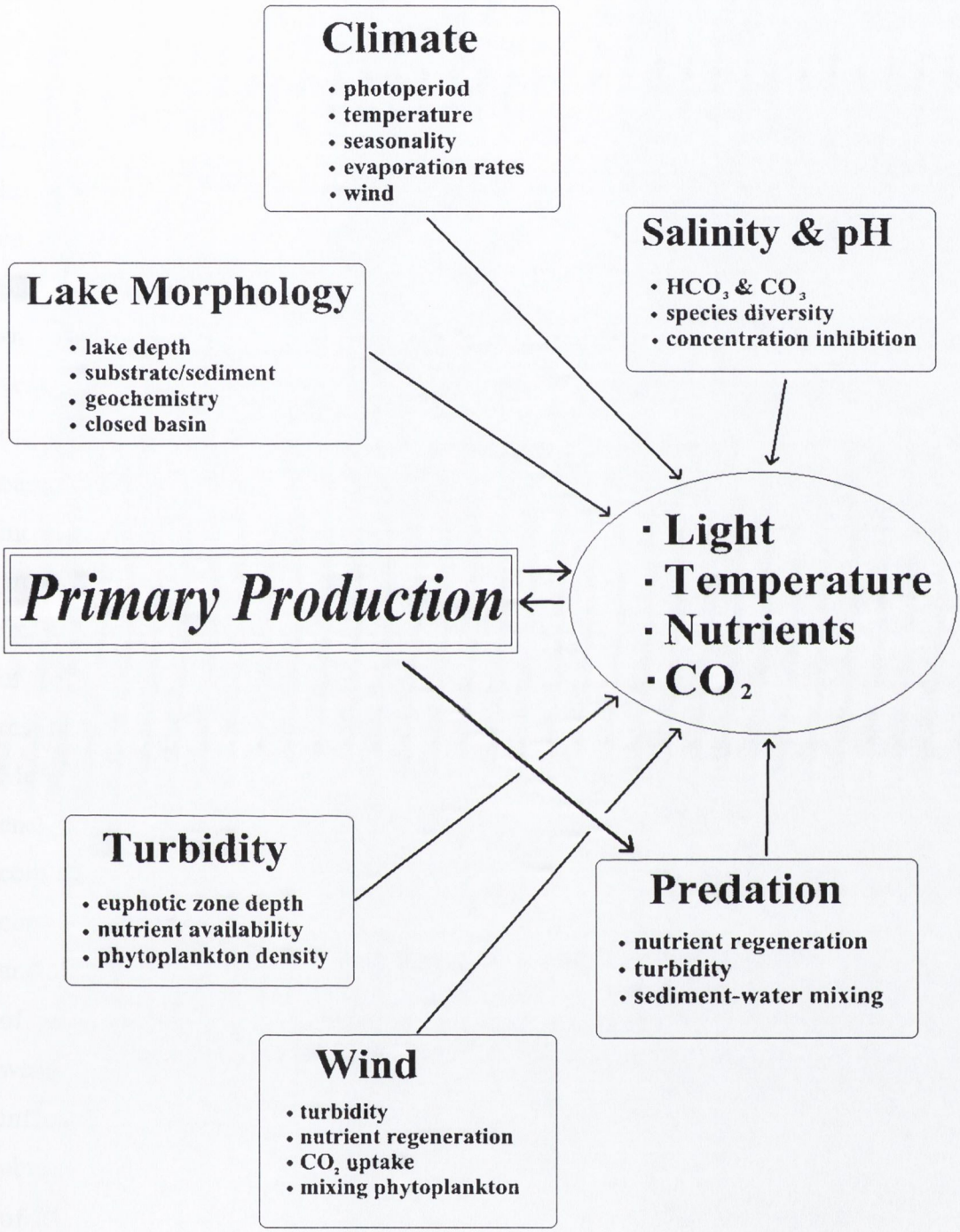

Figure 4.12 Flow diagram of the important physical and chemical factors controlling net primary production on Sua pan.

The climate of Sua pan (Chapter 2) controls the amount of flooding on the pan and, therefore, lake depth during the flood period. Evaporation rates control the flood periods of the lakes and the rate of salinity increase, influencing the rate and period of productivity (e.g. Iltis, 1973; 1974; Vareschi, 1982; Grobbelar, 1985; Melack, 1988). Lake depth appeared to be the overriding controlling factor affecting primary production because it controlled the amount of incident light, temperature and nutrient and ionic concentrations that affect primary production. Rapid decreases in lake depth and area (Chapter 2) coupled with dramatic increases in salinity (Chapter 3) were associated with an increase in productivity in all three basins and a reduction in production late in the very shallow stages of the floods in the middle and south basins. Daily production reached high rates very rapidly in the middle and south basins compared with the north basin (Fig. 4.7) owing to the shallower waters in these basins, higher temperatures and increased sediment-water interactions. Salinity was positively correlated with estimated production and while this correlation may have been concurrent with the positive effects from increased light and temperature as the lake depth decreased, higher concentrations of HCO_3^- and CO_3^{2-} in these waters (Chapter 3) may have provided additional CO_2 reserves in an otherwise CO_2 limited environment (Talling *et al.*, 1973; Vareschi, 1982; Melack, 1988; Harding, 1997). Production estimates did, however, decrease towards the end of the flood periods in the middle and south basins as a result of lower chlorophyll *a* concentrations in the water column owing, perhaps, to intolerance of highly saline conditions or photo-inhibition. Significant increases in production with higher nitrogen and lower total dissolved phosphorus concentrations (Chapter 3) highlight the importance of available nutrients on phytoplankton production. As the lakes decreased, nutrients were concentrated. Temperature differences between summer and winter may have influenced production rates, particularly, in the north basin where phytoplankton abundance increased from below 100 mg chl *a* m^3 in the winter of 2000 (air temperatures of 21-26°C) to concentrations exceeding 300 mg in November 2000, when temperatures were at their highest (32-41°C). An increase in nutrient concentrations may have also, however, influenced this increase (Chapter 3). Changes in salinity and pH (Chapter 3) and lake depth (chapter 2) during this period were negligible. The effect of changes in temperature on primary production in Sua pan is unclear from this study and it may be

that, with winter maximum daily temperatures rarely recorded below 20°C, the effect of such a decrease in temperature on very shallow waters would be difficult to detect. High nutrient concentrations in the latter stages of the flood periods may have been a result of evaporative concentration (Chapter 3) as the shallow waters dried up. The high concentrations of grazing Lesser Flamingo in these disappearing waters would have also ensured the rapid turnover of nutrients, that sustained high periphyton productivity (Moriarty *et al.*, 1973, Vareschi, 1978). The influence of predation on rapid primary producers in such a highly productive lake system highlights the importance of the top-down effect predators have on ecosystem functioning and energy flow rates between the trophic levels. Turbidity also decreased and light incidence increased allowing high perphytic productivity. When the basins got shallower, frequent wind-induced mixing was likely to have increased nutrient recycling from the sediment (Chapter 3).

Productivity rates in the periphyton are likely to vary considerably more than phytoplankton productivity owing to the high and sometimes rapid variations in turbidity and lake depth which controls light incidence (reviewed in Talling & Lemoalle, 1998). Daily periphyton production (Fig. 4.10) based on phytoplankton specific rates may, therefore, be overestimates. The negative correlation between the production of the periphyton community and lake depth, with production increasing as the lakes became shallower indicates the importance of light penetration to the sediment layer and suggests lake depth was also the primary controlling factor for periphyton production. This is most evident when production estimates in the shallow sections of the north basin were estimated to be three orders of magnitude higher than those from the deep sections (Fig. 4.10). Total periphyton production estimates on Sua were very high and were over three times higher than phytoplankton production estimates during both wet seasons.

4.4.6 Conclusions

The flora of Sua pan consisted of phytoplankton algae and cyanobacteria and periphyton associations (often occurring as dense benthic mats) of diatoms and cyanobacteria. Domination by the filamentous cyanobacteria and diatoms is consistent with

phytoplankton composition in similar shallow, often temporary, saline lakes in Africa. The periphyton associations were, however, unusual to this lake type and can be attributed to the extreme shallow nature of the lake.

Phytoplankton abundance and productivity on Sua pan varied considerably among the three basins and within each basin over the flood periods of the 1999-2000 and 2000-2001 wet seasons. In general, they were among the highest estimates recorded anywhere in Africa and maximum abundance and productivity rates were similar to those in some of the most productive lakes in Africa. This is attributed to physical and chemical factors such as favourable light, temperature and nutrients, specifically:

1. Lake morphology, which influenced water depth and area and provided a source of sediment derived turbidity and nutrients;
2. Climate, which controlled seasonal variation of light, temperature, and evaporation rates;
3. Geochemical and evaporative concentration of salinity and pH, which controlled species diversity and abundance aswell as CO_2 availability;
4. Turbidity, which controlled the depth of light incidence and determined the euphotic zone, and increased nutrient availability; and
5. Wind, which controlled turbidity, nutrient regeneration and probably CO_2 uptake.

Periphyton abundance and productivity was considerably higher than that of phytoplankton, particularly in the very shallow conditions near the shores and at the end of the flood periods. The high abundance of diatoms and cyanobacteria and the large areas of Sua pan make the site important for primary production. This provides the basis for supporting large numbers of Lesser and Greater flamingos feeding, respectively, on algae and crustaceans. These aspects will be investigated in Chapters 5 and 6.

Chapter 5

Crustaceans and secondary production

5.1 Introduction

5.1.1 Crustaceans in intermittent saline lakes

Crustacean survival and species richness in intermittent saline lakes depends on the amount and period of flooding and, hence, lake size, which is proportional to flood longevity (Ebert & Balko, 1987; Fryer, 1985). Salinity is also a very important determinant of species richness and composition and, over the total salinity range species richness decreases with increasing salinity (Hammer, 1986; Williams, DD., 1987; Green, 1993; Williams *et al.*, 1990, 1998). Among the saline lakes of East Africa, for example, copepoda and anomopoda species numbers decline dramatically above a conductivity of 1000 μs cm^{-1} (La Barbara & Kilham, 1974; Green, 1986; 1993). *Lovenula africana*, being the most saline tolerant copepod with a salinity tolerance of between 3350 and 15000 μs cm^{-1}, is dominant among the more saline lakes in the region (La Barbara & Kilham, 1974). *Moina belli* is the most tolerant anomopoda, tolerating salinities of up to 21000 μs cm^{-1} (Green, 1993). At low salinities, broad tolerances to salinity among crustacean species are found, while inhibition by lethal concentrations of certain ions (e.g. fluoride) or by the disappearance of specific food sources may result in crustacean paucity at very high salinities (La Barbara & Kilham, 1974; Green, 1993).

In comparison with fresh water species, information on the crustaceans of inland temporary salt lakes in southern Africa is sparse (Allanson *et al.,* 1990; Seaman *et al.,* 1991; Allan *et al.,* 1995). Pioneering studies by Hutchinson *et al.* (1932), and subsequent reports of zooplankton distribution and community structure (e.g. Kok, 1974; Scott *et al.*, 1980; Hart, 1986; Seaman & Kok, 1987; Seaman *et al.,* 1991; Seaman *et al.,* 1999) have shown that species diversity among copepoda and anomopoda, in particular, is ubiquitously low in temporary saline lakes throughout the sub-continent. Numerous species among these groups appear to have opportunistic tolerance to elevated salinities but only some can be truly associated with temporary saline pans (Seaman *et al.,* 1991; Rayner & Heeg, 1994; Allan *et al.,* 1995; Seaman *et al.,* 1999; Rayner, 2001). Most

phyllopods and some species of ostracoda are associated, and sometimes dependent on, temporary saline or hyper saline conditions (Martens, 1988; Day, 1990; Martens *et al.*, 1996; Brendonck & Riddoch 1997).

The first species list of aquatic fauna for the intermittent waters of the Makgadikgadi saltpans is from 1957 (reported by Eccles, undated). In this report a total of ten species of crustacean were identified from the main pan, along with seven other macroinvertebrates, four of which were identified to species level. Many of the species described in these waters have not been reported elsewhere in southern Africa. Species composition on Makgadikgadi is, therefore, unique among inland saline lakes in southern Africa (Seaman *et al.,* 1991). Subsequent identifications of ostracoda (Martens, 1988), and anostraca (Brtek, 1967; Brendonck & Riddoch, 1997) from the pans have confirmed the presence of some of the species identified in Eccles' report. Some of the crustaceans found on Makgadikgadi, although absent in southern African lakes, are found in some alkaline lakes of East Africa (e.g. La Barbara & Kilham, 1974; Vareschi & Vareschi, 1984; Green, 1986). Although no ionic chemistry data was presented in the Eccles report, the pH of the waters that were sampled on Makgadikgadi was high and it has been suggested that similar alkalinities to those in the lakes of East Africa, and proximity to East Africa may be the reasons for a similar species composition (Seaman *et al.,* 1991).

5.1.2 Crustacean abundance and production

Among shallow saline lakes in central and East Africa, seasonal changes in zooplankton abundance occur, predominantly, with hydrological cycles and changes in abiotic factors such as turbidity, nutrient concentrations and temperature (Kalk, 1979*a*; *b*; Saint-Jean, 1983; Hart, 1985; Vareschi & Jacobs, 1984). Salinity has, however, a more important influence on abundance at low water levels (e.g. Kalk, 1979*a*; *b*; Vareschi & Vareschi, 1984; Melack, 1988). Zooplankton biomass estimates in lakes Chad, Awasa, Naivasha and Nakuru, are among the highest recorded for saline lakes in Africa, with high estimates of total crustacean production (Saint-Jean, 1983; Gras & Saint-Jean, 1983;

Mavuti, 1994; Vareschi & Jacobs, 1984; Mengestou & Fernando, 1991). Biomass determines production per unit area, and both biomass and turnover rates (P:B ratios) follow marked seasonal patterns and decrease as temperatures decrease during winter months. In tropical saline lakes, high specific production rates owing to high temperatures and food availability year round lead to some of the highest annual production estimates of crustaceans among African lakes (e.g. Gras & Saint-Jean, 1983; Vareschi & Jacobs, 1984).

While information on faunal assemblages is lacking, biomass or production estimates from natural inland lakes and saltpans in southern Africa is even more sparse (Allanson *et al.,* 1990). Although they reported on zooplankton richness in a number of inland saline lakes, Hutchinson *et al.* (1932) gave no quantitative estimates of the zooplankton communities. Berry (1972) reported very high numbers (5000 individuals l^{-1}) of a *Moina* species in 'pan slush', when the lake was very shallow. Among other lake types in southern Africa, the highest estimates of zooplankton biomass have been reported in eutrophic dams and reservoirs, with mean annual biomass up to 2.8 and 5.32 g m^{-2} d^{-1} (dry weight) in, respectively, Bospoort and Hartbeespoort dams (Seaman *et al.,* 1981). High zooplankton biomass in these reservoirs and dams is, generally, correlated with high concentrations of chlorophyll *a* and trophic status (Seaman *et al.,* 1981; Allanson *et al.,* 1990), although low zooplankton biomass has been, for example, associated with high inorganic turbidity or high densities of inedible cyanobacteria (e.g. Jarvis, 1986; Hart, 1987). Other factors such as alternative food sources, and predation complicate these patterns even further (Talling & Lemoalle, 1998).

Estimates of zooplankton production have been made for only a very few lakes (e.g. Hart & Allanson, 1975; Kalk, 1979*a*; Leveque & Saint-Jean, 1983; Hart, 1987). In Lake Chad, for example, maximum crustacean production correlates with high primary productivity, low turbidity and high temperatures, with total daily production ranging between 10 and 70 mg m^{-3} d^{-1} and annual crustacean production reaching as high as 44 g m^{-2} yr^{-1} (Gras & Saint-Jean, 1983). Turnover rates (P:B ratios) estimated by Hart (1987) for a handful of anamopoda species in Lake Le Roux (a turbid sub-tropical reservoir) were higher than

universal coefficients given by Waters (1977), suggesting high specific productivity among turbid, nutrient rich lakes.

5.1.3 Aims and objectives

The objective of this chapter is to report on identification and estimates of crustacean community biomass and production on Sua pan. This provides an understanding of a link in the food chain and its importance as a food source for the Greater Flamingo population. The aims of the work were to:

1. establish an effective sampling regime for zooplankton and zoobenthos in the three basins of Sua pan during two wet seasons;
2. identify and quantify abundance of species present in the crustacean community and
3. calculate weekly biomass of the common crustacean populations using dry weight and length-frequency analyses in order to estimate total crustacean standing stock throughout the seasons;
4. determine life histories of the larger crustacean species, *Branchinella spinosa* and *B. ornata*;
5. calculate weekly production of the most common crustacean species and estimate total seasonal production for the crustacean community, and relate crustacean production to both primary productivity and Greater flamingo breeding success.

5.2 Materials and methods

5.2.1 Sampling, identification and enumeration

5.2.1.1 Sample techniques

Weekly samples of invertebrates were collected in each basin during the 1999-2000 (1st of November 1999 to 31st of September 2000) and 2000-2001 (1st of November 2000 to 16th of June 2001) wet season. Samples were collected at the five random sample sites chosen for phytoplankton and periphyton samples (Chapter 4). When it was impossible to cover the total area of lake at peak flooding, samples were chosen from designated areas in each basin during the year 2000 and on the north basin during part of 2001 (Fig. 4.1). On each occasion, the water depth was measured and quantitative sampling was carried out using two methods at each sample site;

1. Sweep net technique: a standard 240 μm sweep net (25 cm wide) was used to sample the entire water column or, when deep, the top 25 cm of the water column. On each occasion a one meter sweep was taken, with the length of the sweep measured using a meter stick. The volume of water sampled was calculated as: 1m x 25 cm x 25 cm (net depth) or water column depth (when less than 25 cm). The contents were preserved in excess 80% industrial alcohol.

2. Perspex tube technique: a 1 m long Perspex tube (diameter 5.5 cm), used to sample shallow lakes or ponds (Edmonson & Winberg, 1971), was dropped vertically through the water column to the lake bottom taking an integrated sample of the entire water column. The tube was then bunged at the top and bottom and the contents transferred to a graduated bucket. 5 l of sample were taken on each occasion and then concentrated by passing the water through a 70 μm mesh net. The concentrate was preserved in excess in 80 % industrial alcohol.

5.2.1.2 Identification and enumeration

In the laboratory, samples were transferred to a 500 ml plastic bottle and diluted to 250 or 500 ml of water depending on concentrations of invertebrates or sediment or both. Samples were mixed thoroughly and 5 ml sub-samples, taken with a wide-bore piston-pipette (Bottrell *et al.*, 1976; Wetzel & Likens, 1991), were transferred to a Perspex disc counting chamber with a 5 ml capacity groove around the circumference and counted under a dissecting microscope. Species were identified according to Day *et al.* (1999; 2001), Brendonck & Riddoch (1997), Martens (1984, 1988, 1990*a* & *b*) and Martens *et al.* (1996). Verification of ostracoda identification was given by K. Martens (Royal Belgian Institute of Natural Sciences, Brussels).

In order to test that sub-samples were representative of the sample, agreement with a random distribution was tested statistically by comparing the variance to mean ratio, or index of dispersion (*I*), using the equation;

$$I = s^2 / \bar{x} (n - 1)$$

where s^2 is the variance, $\bar{x}$ the mean and (n - 1) degrees of freedom with n being the sample size (Elliot, 1977; Wetzel & Likens, 1991). *I* approximates unity if there is random distribution and the significance of departures from unity were assessed by reference to Chi squared tables. Comparisons of samples with varying degrees of density, from which ten successive sub-samples were counted, showed varying degrees of departure from a random distribution for all species (Table 5.1).

Table 5.1 Mean ($\bar{x}$), coefficient of variation (C.V.), and index of dispersion (*I*) for the different species of crustaceans from counts of ten successive 5 ml sub-samples at different population densities. The probability (p) of random distribution among sub-samples is also indicated.

Species	$\bar{x}$	C.V.	*I*	p>
Anostraca	11.1	0.59	3.85	0.5
	4.2	0.95	4.51	0.1
	13.3	0.54	3.93	0.5
	27	0.49	6.34	0.1
Moina	2.4	1.40	4.78	0.1
	39.7	0.17	4.21	0.1
	138	0.14	4.56	0.1
Daphnia	12.6	0.43	2.44	0.5
	94	0.12	4.56	0.1
Calanoida	11.4	0.58	3.88	0.5
	39.4	0.35	6.48	0.1
	62.1	0.25	4.86	0.1
Ostracoda	3.2	0.91	4.31	0.1
	166	0.1	1.7	0.5
Conchostraca	38	0.24	2.2	0.5

At low densities some species showed high coefficients of variation (C.V.): calculated by the standard deviation (s) to mean ($\bar{x}$) ratio and expressed as a percentage;

$$C.V. = (s / \bar{x}) \times 100$$

C.V. of sub-samples with a mean of less than 5 individuals exceeded 80%. When mean densities were above 20 individuals per sub-sample, however, C.V. was less than 20%, and between 5 and 15% above a mean of 50 (Fig. 5.1). During sub-sampling, at least 50 individuals of the most common species were counted from 2-5% of the sample and when populations were low, at least 20% of the sample was sub-sampled. It was impossible to sub-sample anostraca adults with a 5 ml pipette owing to their large size

and total numbers of adults per sample were, therefore, transferred to a Petri dish after sub-sampling and counted. In addition, numbers of eggs were counted in both egg-bearing female clutches and those loose in the sample.

Numbers of each species per m^3 were calculated for each tube sample and then converted to numbers per m^2 using the equation:

$$(A_s/a \times n) \times 200 \times d,$$

where A_s is the volume each sample was made up to, a is the volume sub-sampled, n is the number of individuals counted in a, multiplied by 200 to convert numbers per 5 l to numbers per m^3, and by d, the lake depth at the sample site, to convert to numbers m^{-2}. Numbers per m^3 and m^2 for net sweep samples was calculated by:

$$((A_s/a \times n) \times 1/V) \times d, \text{ or } d/0.25 \text{ m},$$

where V is the volume of the sample (calculated by equation on p.5), multiplied by lake depth (d) when the lake depth was below 0.25 m (the depth of the net), or by d / 0.25 m, when the depth of the sweep net was above 0.25 m.

Mean population estimates were then calculated from five random samples on each occasion, for both sampling methods. In order that the data approximate normal distribution, the counts were log transformed before 95% confidence limits were calculated since variance was considered large compared with means in, typically, clumped distributions (Elliot, 1977; Bottrell *et al.*, 1976).

Mean weekly abundance estimates from five random samples were calculated for each sampling technique and used to calculate mean seasonal abundance for each flood period. Significant differences in mean weekly abundance estimates between net sweep and tube sampling techniques were tested using Repeated-Measures ANOVA analyses for each species. Sample date, a 'fixed' factor, was 'nested' in sample technique and provided for repeated measures on sample date.

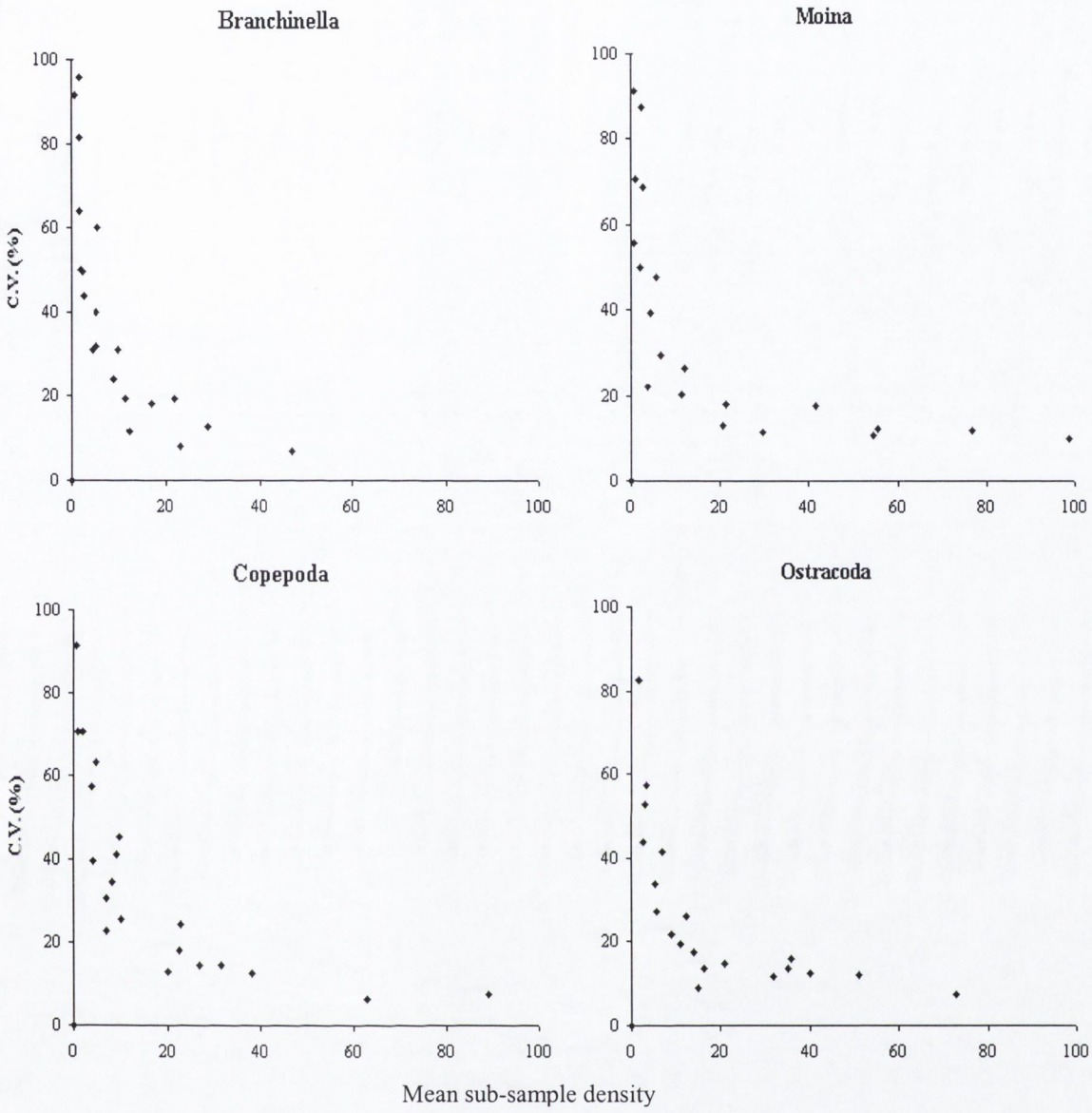

Figure 5.1 Relationship between coefficient of variation and the mean density of the most common crustaceans on Sua pan: anostraca, *Moina*, copepoda and ostracoda, per 5 ml sub-sample taken with a wide-bore pipette.

5.2.2 Population length frequencies

During weekly counts at least 100 and, occasionally, over 150 individuals of the most common crustaceans were measured using a calibrated eyepiece graticule. For practical reasons, ostracod species were included together as one group. When population densities were small, all individuals were measured. Anostraca (≤ 28 mm) were measured from the top of the head to the tip of the cercopods, and calanoids (≤ 3 mm) were measured from top of the head to the base of the furcal rami. *Moina* and *Daphnia* were measured from top of the head to the base of the abdominal setae and carapace spine, respectively. Ostracoda and conchostraca were measured along the longitudinal length of the valves.

5.2.3 Crustacean biomass

5.2.3.1 Dry weight analyses

During the 2000-2001 wet season, crustaceans were also collected from each basin for dry-weight analyses. In the first two weeks of the 2000-2001 wet season, random samples were taken every two days using the Perspex tube and weekly thereafter, using the sweep net method until the animals reached maximum size. Not all species emerged at the beginning of the flood and sampling continued on a bi-weekly basis throughout the flood periods. With no access to a microbalance in Botswana, samples were preserved in 5% formalin for dry weight analyses on return to Dublin, at least six months later. Dry weights could not be calculated for *Daphnia barbata* and the conchostracan *Leptestheria striatoconcha*, owing to an absence of these animals from Sua pan during the 2000-2001 wet season.

For estimates of dry weight, samples were washed with distilled water and individuals of each species measured under a dissecting microscope. Smaller animals were assigned to 0.1 mm classes. Anostraca were assigned to classes that ranged from 0.2 mm, in the early life stages, to 1, and 2 mm classes as they increased in length to maturity. Individuals

were placed on pre-weighed tinfoil, oven-dried at 60°c for over twenty four hours and weighed on a SARTORIUS electronic Microbalance®, to a precision of 0.1 μg. It was assumed dry weight loss resulting from formalin preservation was negligible (Bottrell *et al.*, 1976). Smaller individuals and eggs were weighed together in batches of 10 and 20 per sheath of tin foil. Between 5 and 20 individuals from each size class were measured, weighed and the results log-transformed before the relationship between length and weight was analysed by regression for each species.

5.2.3.2 Species-specific standing crop biomass

Weekly population lengths (mean) for each species were converted into weekly standing crop biomass (mg m^{-2}) using species-specific length-weight relationships:

$$\ln W = \ln a + b \ln L$$

where lnW is the natural logarithm of dry weight (μg), ln a is the estimate of the intercept, b the estimate of the slope and ln L the size class geometric mean in the sample population each week. Both species of anostraca had very similar length-weight relationships (Table 5.2) and these were, therefore, pooled to calculate biomass for each population. The most common species of ostracoda were similar in size and weight and weekly mean abundance for all species were converted to biomass using pooled length-weight relationships. Mean weights (μg) for anostraca and calanoida eggs and *Moina* ephippia were calculated from replicate dry weights and multiplied by the mean number of eggs and ephippia per female, which included eggs in ovigerous female clutches and those loose in the sample, resulting in mean weekly reproductive biomass per female. Measured neonates, from parthenogenic anamopoda, were converted to biomass using the *Moina* regression equation. Because of their absence from dry weight samples, *Daphnia* dry weights were calculated using a length-weight relationship for *D. longispina* from Bottrell *et al.* (1976):

$$\ln W = \ln 1.073 + 2.892 \ln L$$

This species was considered similar in morphology and size range (0.6 to 2.35 mm) to *D. barbata* and the equation was based on the total length excluding the caudal setae of preserved individuals. Owing to their absence from dry weight samples and with an

absence of L-W relationships for the species in the literature weekly dry weight data for conchostracans were not estimated.

Table 5.2 Mean weight (mg) of *B. spinosa* and *B. ornata* individuals from a range of size classes, taken from the middle basin during the 2000-2001 wet season.

Size Class (mm)	B. spinosa	B. ornata
2.5	0.01	0.01
3	0.02	0.02
3.5	0.03	0.02
4	0.04	0.04
4.5	0.05	0.06
5	0.06	0.06
5.5	0.06	0.07
6	0.07	0.07
6.5	0.10	0.10
7	0.14	0.14
7.5	0.17	0.16
7.5	0.16	0.16
8	0.21	0.20
8.5	0.24	0.25
9	0.31	0.32
9.5	0.40	0.39
10	0.49	0.53
10.5	0.54	0.58
11	0.65	0.69
11.5	0.60	0.62
12	0.70	0.72
12.5	0.75	0.79
13	0.84	0.83
13.5	0.85	0.84
14	0.87	0.88
15	1.01	1.01
16	1.03	1.09
17	1.27	1.34
22	2.49	2.56
23	3.11	3.15
26	3.57	3.63

5.2.4 Secondary production

5.2.4.1 Anostraca production

It was possible to identify cohorts among populations of both anostracan species during each season. Production, P, was calculated from length frequencies using the 'growth increment summation' method (Rigler & Downing, 1984), whereby increases in average weekly cohort biomass were multiplied by mean cohort density;

$$P = N_{1.2}(m_2-m_1) + N_{2.3}(m_3-m_2) + \ldots + N_{(k-1).k}(m_k-m_{(k-1)})$$

where $N_{1.2}$ is the geometric mean of the population density over the time between the first weekly sample and the second, m_1 is the mean biomass of an individual from the first sample and k is the number of sampling dates in the lifetime of each. Reproductive production was calculated separately as the weekly increase in the mean biomass of eggs multiplied by the geometric mean of female density between samples and the results added to total weekly production estimates. To account for the input from the previous generation, mean egg dry weight multiplied by the number of hatchlings in the first sampling week was subtracted from the first weeks production estimate. Mean daily P:B ratios for both species of anostraca were calculated from cohorts and used to estimate production on occasions when sparse data sets could not be assigned to cohorts.

5.2.4.2 Crustacean production using P:B ratios

Weekly biomass estimates for *Moina, Daphnia,* and the calanoid copepoda were converted to production estimates using daily P:B ratios (specific production rates) from the literature (Table 5.3).

Table 5.3 Daily P:B ratios for species, from the literature used to convert weekly biomass estimates of *Moina*, *Daphnia*, copepoda, ostracoda and conchostraca to production estimates. The figure marked with * was calculated from a regression equation (see text).

Species	Daily P:B ratio	Author
Moina micrura	0.52	(Leveque & Saint-Jean, 1983)
Daphnia barbata	0.008	(Hart, 1987)
Lovenula africana	0.048	(Vareschi & Jacobs, 1984)
Ostracoda	0.33*	

Specific production figures for lacustrine ostracods were absent from the literature. The relationship between mean adult dry weights and corresponding mean daily P:B ratios (Fig 5.2) for small tropical and sub-tropical crustaceans and rotifers, taken from the literature (Table 5.4), was, therefore, used to estimate a mean daily P:B ratio for ostracoda using the linear regression equation;

$$\log P:B = -1.885 (- 0.134 \log W)$$

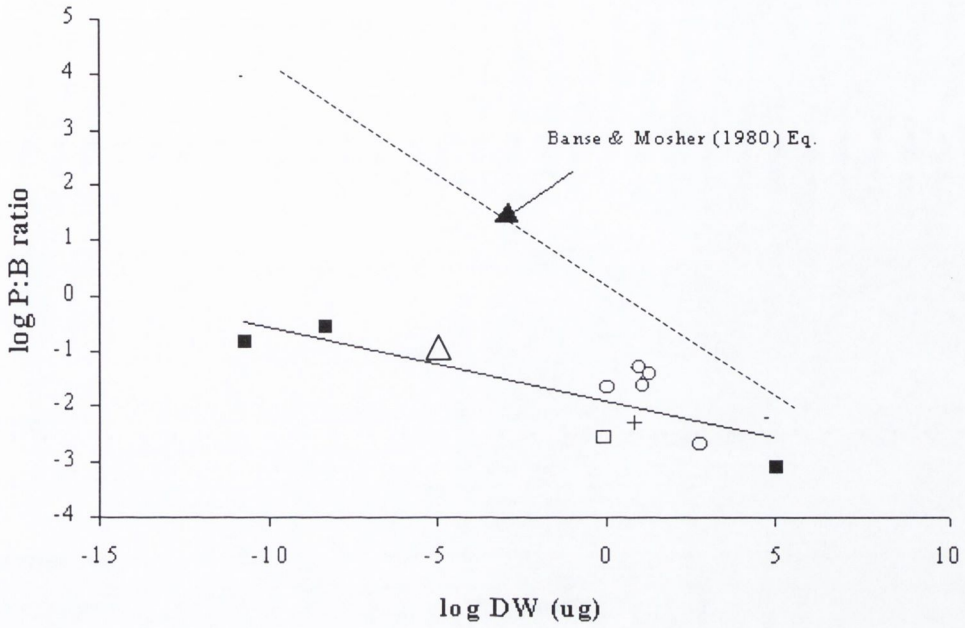

Figure 5.2 Linear regression relationship between mean adult dry weight and mean daily P:B ratio for a number of small invertebrates in the tropical shallow lakes of George □, Kinneret + ,Chad ○, and Nakuru ■, taken from the literature (Table 5.4), where r^2 is 0.61, RMS is 0.3, F-ratio is 12.6, $p \leq 0.007$ and n is 10. Broken line represents the equation log P:B = a - b log W for the relationship between P:B ratios and the mass of small invertebrates in temperate lakes that reach maturity in less than one year (Eq. 5, Table 2, Banse & Mosher, 1980). The triangle △ represents the approximate P:B- dry weight relationship estimated for ostracods.

Total seasonal production for each species was calculated by the summation of the daily production:

$$\text{Seasonal } P = P_1.P_2\,(Sd_2\text{-}Sd_1) + P_2.P_3\,(Sd_3\text{-}Sd_2) + \ldots + P_{(k\text{-}1)}.P_k\,(Sd_k\text{-}Sd_{(k\text{-}1)})$$

where $P_1.P_2$ is the geometric mean daily production rate between sample week one and two, Sd_2-Sd_1 is the number of days between sample date one and two, and k is the number of sampling dates in each season.

Table 5.4 Mean adult dry weight and equivalent mean annual P:B ratios of a number of crustaceans and rotifers estimated from a number of tropical and sub-tropical shallow lakes. Mean dry weights of two species of diaptomid and two cyclopoids (notated by *) correspond to mean daily P:B ratios from the same year in Leveque & Saint-Jean (1983). Dry weight estimates from size distribution in the lake (notated by *s*). Method for estimating production was Growth Summation (Winberg) method, otherwise that of Edmonson, 1960 (Burgis, 1974).

Species	$\bar{x}$ Adult DW (µg)	$\bar{x}$ daily P:B ratio	Lake	Reference
Thermocyclops hyalinus	0.93	0.078	L. George	Burgis, 1974
Mesocyclops leucarti	1.85	0.1	L. Kinneret	Gophen, 1978
Diaphanasoma excisum	2.5	0.28	L. Chad	Gras & Saint-Jean, 1983
Daphnia barbata	2.9	0.21	L. Chad	Gras & Saint-Jean, 1983
Bosmina longirostris	0.75	0.2	L. Chad	Gras & Saint-Jean, 1983
Diaptomid *	14.2	0.07	L. Chad	Gras & Saint-Jean, 1983
Cyclopoid *	3.35	0.25	L. Chad	Gras & Saint-Jean, 1983
Lovenula africana	149 ^{S}	0.046	L. Nakuru	Vareschi & Vareschi, 1984
Brachionus dimidiatus	0.000022	0.45	L. Nakuru	Vareschi & Vareschi, 1984
Brachionus plicatilis	0.00024	0.57	L. Nakuru	Vareschi & Vareschi, 1984

5.2.4.3 Total seasonal production

Total seasonal production (g m^{-2} yr^{-1}) on Sua pan was estimated by the summation of all crustacean production estimates for each season, in the north, middle and south basins. Total seasonal production for the south basin during the 1999-2000 wet season were the total of eleven weeks out of a total flood period of 10 months and so only represent the first third of the flood period.

5.3 Results

5.3.1 Crustacean taxonomy on Sua pan

Species diversity among the crustaceans on Sua pan comprised eleven species from six different orders, in three classes (Table 5.5). *Metadiaptomus transvaalensis*, *Plesiocypridopsis aldabrae* and *Potamocypris* were rare, occurring in low numbers on occasion and for short periods only in the north basin during the beginning of the 1999-2000 wet season. For this reason they were not included in the abundance and production estimates. Other macro-invertebrates also occurred during all or parts of the flood periods, mainly in the north basin. These included various species of beetle and insect larvae. These are added to the total species list below, although no further abundance or biomass analyses was carried out on them.

Table 5.5 Taxonomic species list of crustaceans and other small invertebrates found on Sua pan between November 1999 and June 2001.

Class	Order	Species	
Crustaceans			
Branchiopoda	Anostraca	*Branchinella spinosa*	(Milne-Edwards 1840)
		Branchinella ornata	(Daday 1910)
	Conchostraca	*Leptestheria striatoconcha*	(Barnard 1924)
	Anomopoda	*Moina belli*	(Gurney 1904)
		Daphnia barbata	(Weltner 1897)
Copepoda	Calanoida	*Lovenula africana*	(Daday 1908)
	Cyclopoida	*Metadiaptomus transvaalensis*	(Methuen 1910)
Ostracoda	Podocopida	*Limnocythere tudoranceai*	(Martens 1990)
		Sclerocypris exserta makarikarensis	(Martens 1988)
		Potamocypris new sp ?	(Martens pers comm.)
		Plesiocypridopsis aldabrae	(Meisch 1988)
Other Small Invertebrates			
		Coryxid hemiptera of genus *Sigara* and *Notonecta*	
		Species of predacious beetle *Dytiscus*	
		Beetle larvae, *Cybister*	
		Dragonfly larvae, Libellulidae	
		Nematode worms	

5.3.2 Crustacean abundance

5.3.2.1 Population abundance

Dramatic spatial and temporal fluctuation of areal abundance of the common crustacean species was found in Sua pan in both study years (Fig. 5.3, 5.4, 5.5 and Table 5.6).

Table 5.6 Mean and maximum weekly abundance (per m^2) ± 95 % confidence limits (CL) of crustaceans in the north, middle and south basin of Sua pan from both sweep net (sw) and tube sample (tb) techniques during the 1999-2000 and 2000-2001 wet seasons.

		North		Middle		South	
Species	**Sample**	**99-00**	**00-01**	**99-00**	**00-01**	**99-00**	**00-01**
Mean							
B. spinosa	Sw	32 ± 23	12 ± 8	677 ± 101	2906 ± 1045	156 ± 52	981 ± 479
	Tb	168 ± 65	56 ± 29	1511 ± 815	3718 ± 1337	148 ± 82	2257 ± 940
B. ornata	Sw	216 ± 93	435 ± 147	224 ± 106	1515 ± 1110	39 ± 20	0
	Tb	138 ± 86	0	2042 ± 1077	2237 ± 777	9 ± 7	0
M. belli	Sw	16505 ± 11151	104184 ± 37318	3068 ± 1187	1385 ± 614	17709 ± 4316	1167 ± 788
	Tb	41222 ± 32205	167169 ± 62329	113742 ± 52594	3163 ± 1120	155772 ± 86600	2108 ± 1172
D. barbata	Sw	19343 ± 9050	650 ± 522	0	0	0	0
	Tb	24784 ± 12728	0	0	0	0	0
L. africana	Sw	60817 ± 20555	18275 ± 6607	385 ± 188	79 ± 114	0	0
	Tb	81490 ± 38790	32728 ± 18180	4685 ± 2880	114 ± 224	0	0
Ostracoda	Sw	656 ± 918	11070 ± 10823	6218 ± 2993	5048 ± 2004	271 ± 150	0
	Tb	1669 ± 1078	54882 ± 29080	215419 ± 98265	3751 ± 1037	13440 ± 8546	0
L. striatochonca	Sw	91 ± 40	0	0	0	0	0
	Tb	212 ± 111	0	0	0	0	0
Maximum							
B. spinosa	Sw	83 ± 43	10 ± 6	11651 ± 625	5583.3 ± 1062	410 ± 67.3	1817 ± 886
	Tb	236 ± 82	56 ± 29	23440 ± 10236	9640 ± 2268	404.8 ± 260.8	2850 ± 1210
B. ornata	Sw	959 ± 477	1130 ± 284	1921 ± 918	2995 ± 1909	105.8 ± 50.1	0
	Tb	490 ± 287	0	22680 ± 11309	3924 ± 458.5	9 ± 7.3	0
M. belli	Sw	107389 ± 106279	580133.3 ± 222528	14600 ± 8414.9	4616.7 ± 1650	79416.7 ± 16880	1167 ± 788
	Tb	230336 ± 191464	722044 ± 214708	779080 ± 176581	9448 ± 3132	621240 ± 262504	2108 ± 1172
D. barbata	Sw	197589 ± 67298	650 ± 522	0	0	0	0
	Tb	188348 ± 78878	0	0	0	0	0
L. africana	Sw	345124 ± 53144	99706.9 ± 43085	1133 ± 432	100 ± 131	0	0
	Tb	429348 ± 84646	181644 ± 159154	16760 ± 9800	264 ± 517	0	0
Ostracoda	Sw	4928 ± 7507	49375 ± 60753	44892 ±13472	11867 ± 4705	292 ± 100	0
	Tb	4480 ± 971	269808 ± 135678	1104600 ± 466968	10092 ± 2516	17520 ± 11099	0
L. striatochonca	Sw		0	0	0	0	0
	Tb	400 ± 226	0	0	0	0	0

In the north basin, the larger crustacean species (sub-class Eubranchipoda), the anostracans *B. spinosa* and *B. ornata* and the conchostracan *L. striatochonca*, were the least abundant (Fig 5.3, and Table 5.6). Anostracan species were most abundant at the beginning of the 1999-2000 wet season (December 1999), although maximum recorded numbers were still two orders of magnitude lower than those of the other crustacean species. Anostracan populations quickly decreased as the season progressed, and both species then disappeared in March-April 2000, and were sampled only on occasion during the rest of the season. Similarly, *L. striatochonca* reached a recorded maximum in December 1999 before it too quickly decreased in numbers and disappeared in mid-March 2000. *M. belli*, in contrast, was one of the most abundant species, with recorded population estimates increasing from approximately 1000 to 100,000 individuals (ind) m^{-2} in the early part of the flood period. The population then decreased and disappeared in March 2000. After a period of absence for much of the 1999-2000 wet season, *Moina* emerged again and became abundant in September 2000, when the population occasionally numbered >100000 m^{-2}. Abundance fluctuated considerably during the 2000-2001 wet season (Table 5.6). After its emergence in January 2000, *D. barbata* became one of the most abundant species with maximum recorded abundance in May 2000. Its disappearance from the north basin occurred in October 2000 soon after *M. belli* emerged again. *L. africana* was consistently abundant throughout the flood period on the north basin and numbers gradually increased during the 1999-2000 wet season. Population estimates of over 100000 m^{-2} were recorded on many occasions with recorded maxima in September 2000. Population numbers then decreased during the 2000-2001 wet season, although a large peak in March contributed to seasonal recorded maxima.

In comparison, ostracods were rare during the 1999-2000 season but became increasingly abundant in the 2000-2001 wet season as the lake decreased in size and depth. Seasonal maxima recorded abundance, which occurred in March 2001, was at least two orders of magnitude higher than the maxima of the previous season. The majority of the population consisted of *Limnocythere tudoranceai*, while *Sclerocypris exserta makarikarensis*, the second most common species, was present at much lower densities. The other two species, *Potamocypris* sp. and *Plesiocypridopsis aldabrae*, were very rare in comparison.

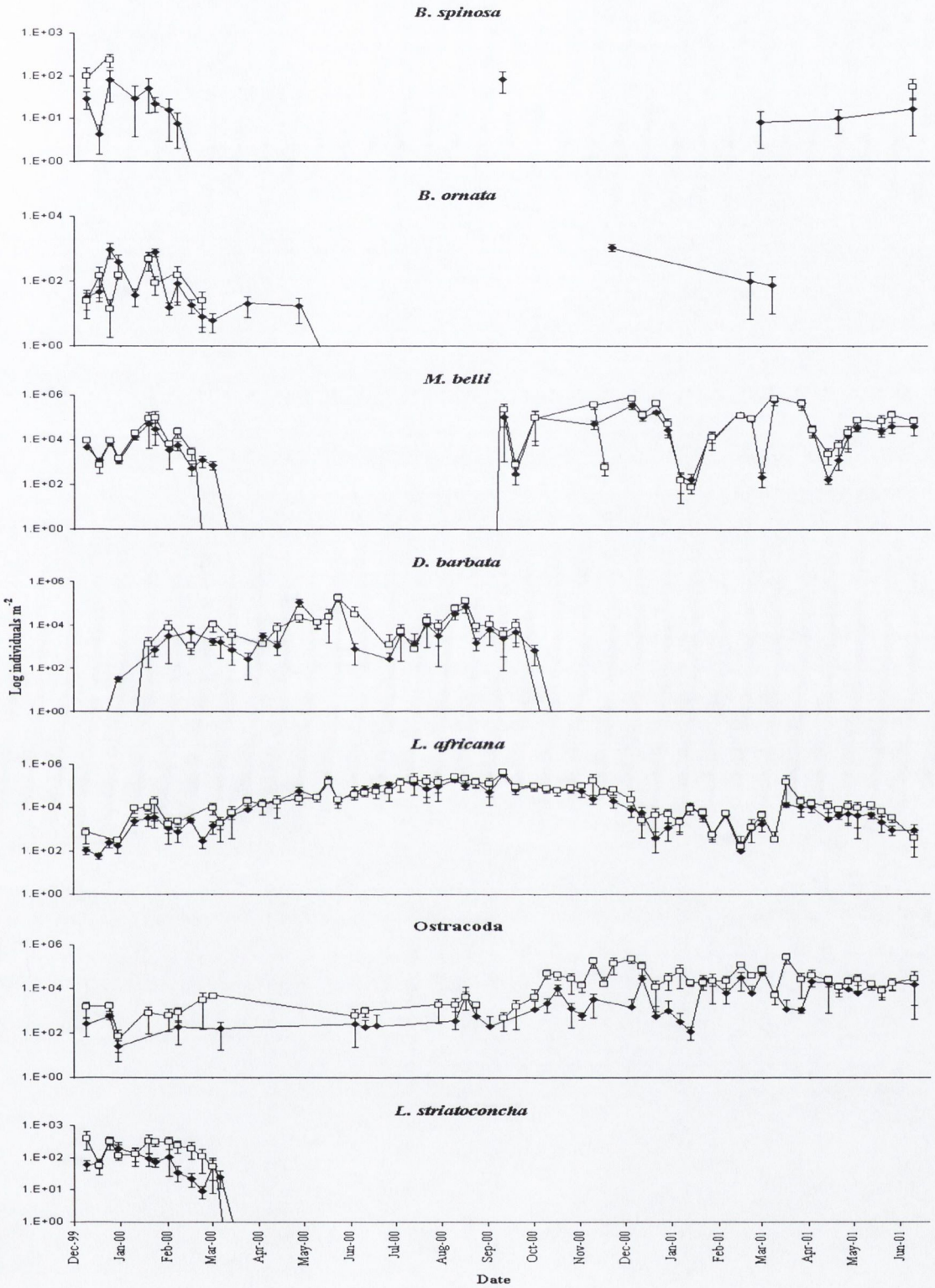

Figure 5.3 Mean crustacean abundance per m^2 (±95% CL) from weekly sweep net◆ and tube □ sampling on the north basin, over the 1999-2000 and 2000-2001 wet seasons.

Species richness was lower in the middle basin compared with the north basin (Fig 5.4 and Table 5.6), while species abundance also varied. Both anostracan species, for example, were more abundant in the middle basin, with higher means and considerably higher maxima. During the 1999-2000 wet season maximum abundances of 20000 m^{-2} for both species were recorded at the beginning of the flood period from tube samples (Table 5.6). A considerable decrease in weekly estimates followed after initial flooding and *B. ornata* disappeared from the basin in April. *B. spinosa*, the dominant of the two species, did, however, increase in numbers again towards the end of the flood period. During the short wet season of 2000-2001 *B. spinosa* abundance was consistently high and maximum abundance occurring in March 2001 (Table 5.6). The population of *B. ornata* quickly decreased and disappeared soon after maximum recorded abundance (Table 5.6) at the beginning of the flood period. Young *B. spinosa* were recorded during a brief flood in December 2000 using the tube technique, with numbers reaching >10000 ind m^{-2}. *M. belli* was the most abundant crustacean species in the middle basin. At the start of the 1999-2000 wet season it had low numbers, which gradually increased to recorded maxima in April (Table 5.6), before the population decreased again as the lake dried up. Abundance was lower during the 2000-2001 wet season, with recorded maxima one order of magnitude less than the previous season (Table 5.6). *L. africana* was rare at the beginning of the 1999-2000 wet season but the population increased between March and June 2000, with maximum abundance occurring in late March 2000 (Table 5.6). The species appeared again during the 2000-2001 wet season, but weekly estimates were considerably lower and maximum abundance was one order of magnitude lower. Ostracods, predominantly of the species *L. tudoranceai*, were again very abundant in the middle basin. Abundance increased from relatively low numbers at the beginning of the 1999-2000 wet season to consistently high values in March, April and May, with recorded maxima occurring in May (Table 5.6). *L. tudoranceai* was consistently abundant again during the 2000-2001 wet season, although mean and maximum numbers were not as high as the previous season (Table 5.6).

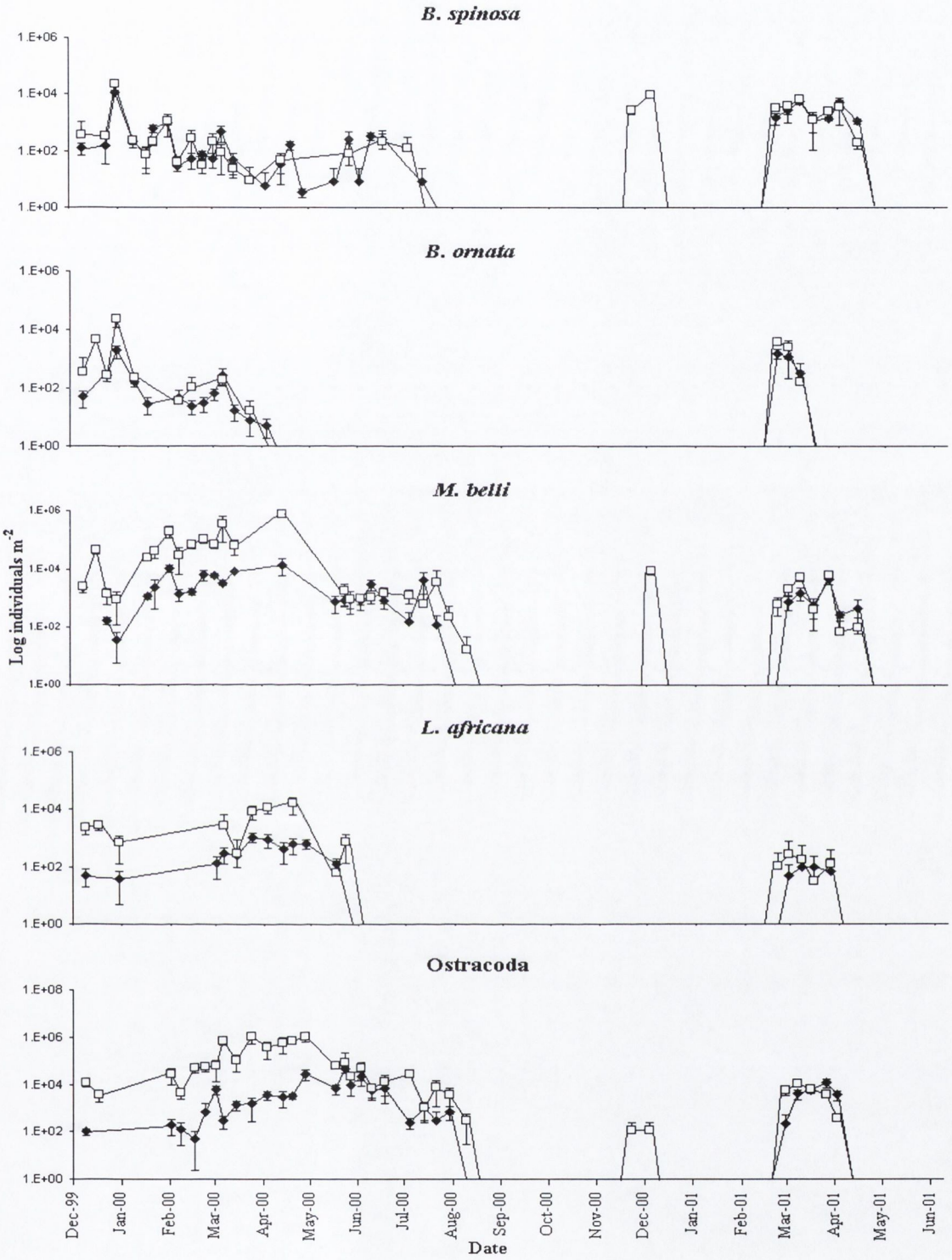

Figure 5.4 Mean crustacean abundance per m^2 (± 95% CL) from weekly sweep net◆ and tube□ sampling on the middle basin, over the 1999-2000 and 2000-2001 wet seasons.

In the south basin, species richness was lower than either the north or middle basins, with differences also found in population abundances (Fig. 5.5 and Table 5.6). *B. spinosa* was the dominant anostracan. Highest abundance was recorded during the 2000-2001 season with recorded maxima occurring in March 2001 (Table 5.6). *B. ornata* was only present in low numbers at the beginning of the 1999-2000 wet season (Fig 5.5). *M. belli* was, as in the other basins, the most abundant crustacean, with maxima of > 70,000 (sw) and > 600,000 ind m^{-2} recorded in April 2000. Its presence was brief at the beginning of the 2000-2001 wet season and was recorded at considerably lower numbers (Table 5.6) than the previous year. *L. tudoranceai* was the only other crustacean to appear in the south pan during the 1999-2000 wet season, found for a brief period in May 2000 (Fig. 5.5, Table 5.6).

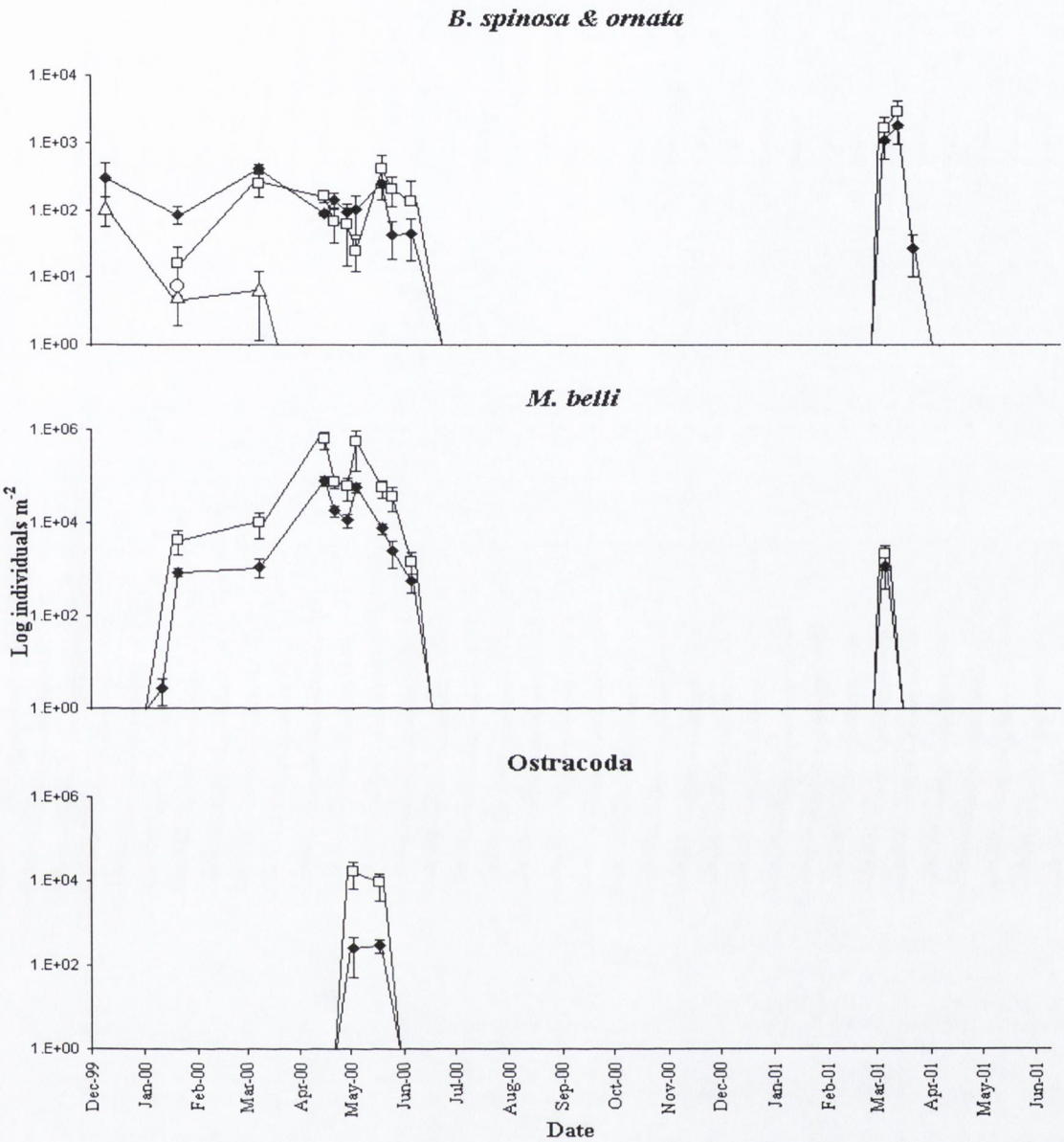

Figure 5.5 Mean crustacean abundance m^{-2} (± 95 % CL) from weekly sweep net samples of *B. spinosa*◆ and *B. ornata*△ and tube samples (*B. spinosa*;□ , *B. ornata*⊙) of the south basin, over the 1999-2000 and 2000-2001 wet seasons.

5.3.2.2 Comparison of sweep net samples and tube samples

Differences in the crustacean abundance between the two sampling techniques are apparent from Table 5.6 and Fig. 5.3, 5.4 & 5.5. Overall comparison of the two sampling techniques is shown in Fig. 5.6.

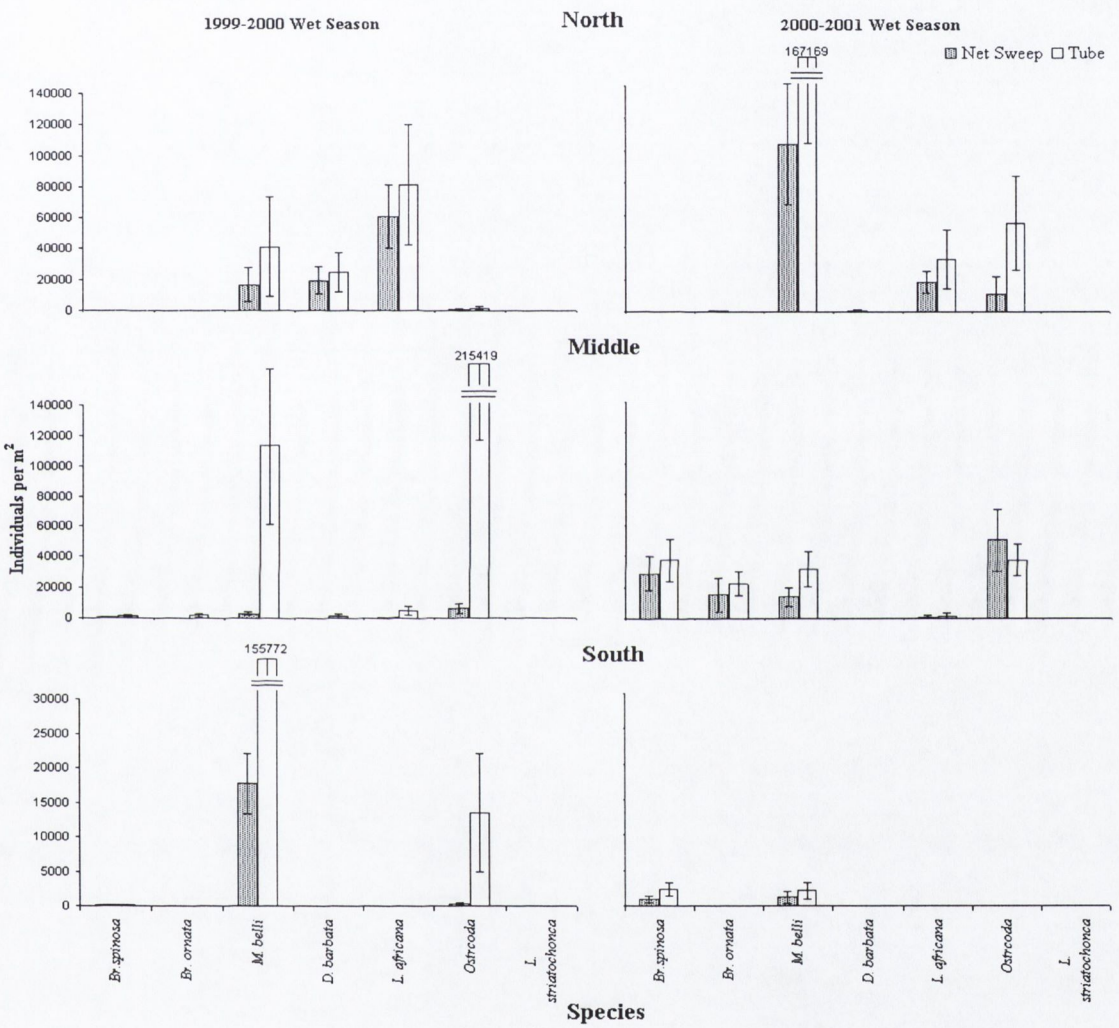

Figure 5.6 Mean seasonal abundance estimates (± 95% CL) for most common crustacean species, from samples using the sweep net▨ and tube□ techniques in the north, middle and south basins, during the 1999-2000 and 2000-2001 wet seasons.

In general, population abundance estimates were considerably higher in tube samples. Consistent differences in captive efficiencies, particularly of *M. belli*, *L. africana*, and ostracods, were most evident during periods of high abundance. While overall mean abundance estimates for both *Branchinella* species were higher among tube samples (Table 5.6), sweep net catching efficiency was considerably higher at low densities, particularly in the north basin (Fig 5.3).

In the north basin, sweep net estimates for *Branchinella*, *D. barbata*, *M. belli* and *L. africana* were slightly higher than estimates from tube samples during the 1999-2000 wet season, while estimates of ostracod abundance were higher among tube samples (Fig. 5.7). These differences were greatly increased during the 2000-2001 wet season. In the middle basin, mean proportional abundance for all species except the ostracods were again higher among sweep net samples, particularly for *M. belli* during the 1999-2000 wet season. Ostracod abundance was considerably higher among tube samples. Mean proportional abundance differences were, however, reversed during the 2000-2001 wet season, with abundance estimates for *B spinosa, M. belli* and *L. africana* all higher in tube samples, while estimates from sweep net samples provided considerably higher abundance estimates for ostracods and *B. ornata*. On the south basin, *M. belli* and ostracod mean proportional abundance was considerably higher for tube samples during the 1999-2000 wet season. Sweep net sampling produced higher abundance estimates for the anostraca species. The pattern of differences was the same during the 2000-2001 wet season, although *B. spinosa* comprised the majority of total crustacean abundance.

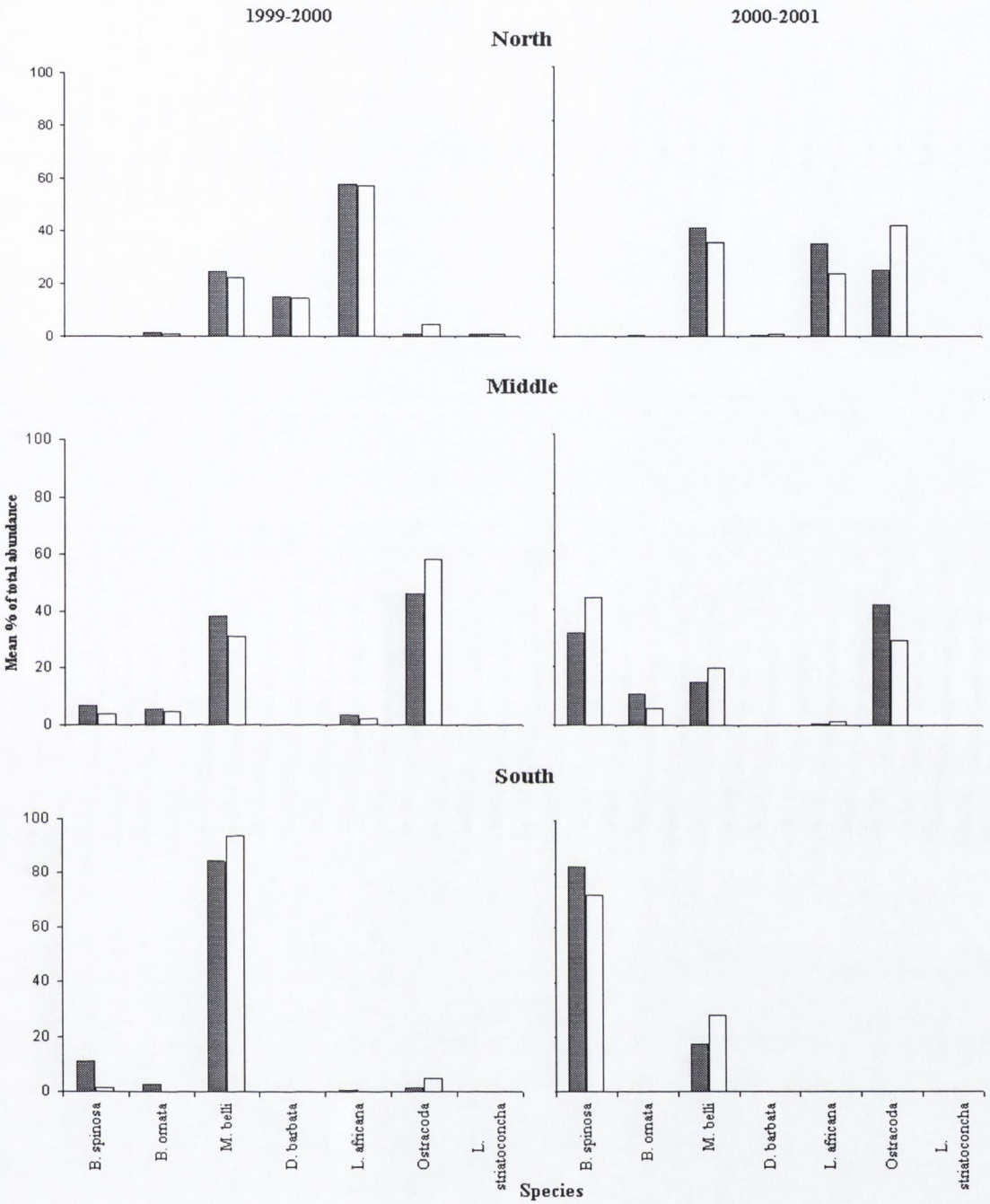

Figure 5.7 Mean proportional abundances of crustacean species found on the north, middle and south basin of Sua pan, using sweep net ▩ and tube □ sampling techniques.

The significance of the differences in crustacean abundance during both wet seasons was tested using RM ANOVA analyses on the weekly abundance results from each sampling technique (Table 5.7). The seasonal mean abundance estimates for all species except *B. ornata* were significantly higher from samples taken with the tube technique. The greatest difference existed in abundance estimates of ostracods.

Table 5.7 F-ratios (*F*), degrees of freedom (*df*) and statistical significance (*P*) of the interaction between sampling technique and sampling day on crustacean abundance in all three basins, over the 1999-2000 and 2000-2001 wet seasons, analysed with RM-ANOVA.

Species	*F*	*df*	*P*
B. spinosa	7.27	1,4	0.008
B. ornata	1.71	1,4	0.197
M. belli	7.74	1,6	0.006
D. barbata	4.62	1,0	0.036
L. africana	4.11	1,4	0.044
Ostracoda	35.9	1,7	0.0001
L. striatoconcha	9.55	1,0	0.005

5.3.3 Length-weight relationships

Length-dry weight regressions, used to convert mean weekly population lengths to weekly population dry weights, all contained significant mean regression lines and low residual mean squares (Table 5.8 & Fig. 5.8).

Table 5.8 Measured species-specific length-dry weight relationships for the most common crustaceans on Sua pan; *Branchinella*, *M. belli*, *L. africana* and ostracoda, used to calculate population specific standing crop biomass. The slope (b), intercept (ln a), F ratio (F), degree of significance (P), number of observations (n), residual mean squares (RMS), and range of lengths measured (mm) are presented for the relationship:

$$\ln W = \ln a + b \ln L.$$

The mean dry weight (μg), with 95 % c.l., of anostraca and copepoda eggs and *M. belli* ephippia are also given.

Crustacean	**ln a**	**b**	**F-ratio**	**P**	**n**	**RMS**	**Range (mm)**	**W (μg) ± 95% cl**
Branchinella	6.4	2.36	14100	0.001	410	0.152	0.4 – 28	
B. egg								4.7 ± 0.4
M. belli	5.01	2.513	1360	0.001	133	0.119	0.4 – 1.6	
Moina ephippia								36 ± 6.7
L. africana	5.34	2.576	2130	0.001	56	0.03	1.0 – 3.3	
L. egg								0.42 ± 0.2
Ostracoda	3.19	3.43	748	0.001	38	0.07	0.3 – 0.8	

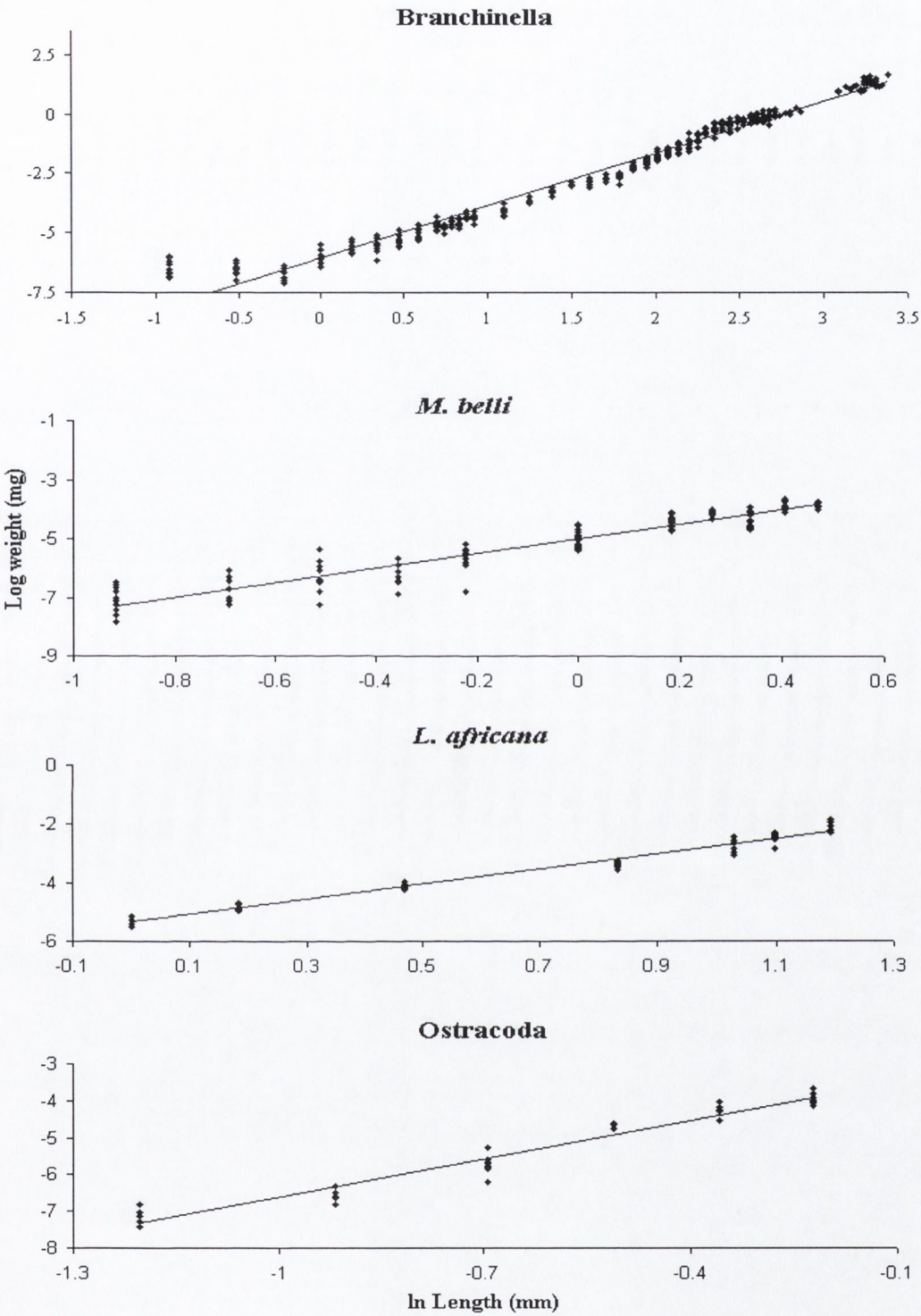

Figure 5.8 Linear regression relationships between length and weight of branchinella, *M. belli*, the calanoid *L. africana*, and ostracoda collected on Sua pan during the 2000-2001 wet season, with variables log transformed.

5.3.4 Crustacean biomass

5.3.4.1 Weekly crustacean biomass and species proportions

In the north basin, *B. spinosa* biomass was one of the lowest during the 1999-2000 wet season, owing to its rarity and low mean weekly abundance, with *B. ornata* estimates higher at the beginning of the season (Fig. 5.9, Table 5.9). Although far more abundant than *B. ornata*, *M. belli* biomass estimates were not much higher than those of *B. ornata* (Fig 5.9). *D. barbata* and *L. africana* biomass, on the other hand, were consistently, at least one order of magnitude higher than anostracan biomass and recorded seasonal maxima were the highest of all crustacean species (Table 5.9). When the two sampling techniques were compared, biomass estimates for *M. belli* and, in particular *L. africana*, were generally well correlated. Biomass estimates for *D. barbata* and the *Branchinella* species were, however, frequently higher from tube samples (Fig 5.9). Tube sample estimates were also considerably higher for ostracods. They comprised relatively low biomass and had the lowest recorded maximum estimates (Table 5.9). The anostracans and *D. barbata* contributed very little biomass owing to their rarity during the 2000-2001 wet season. Weekly biomass estimates fluctuated considerably for *M. belli* (Fig. 5.9) and the seasonal maxima were considerably higher (Table 5.9). Seasonal maxima for ostracod increased by one order of magnitude owing to its increased abundance during that season, while weekly biomass estimates for *L. Africana* decreased (Table 5.9).

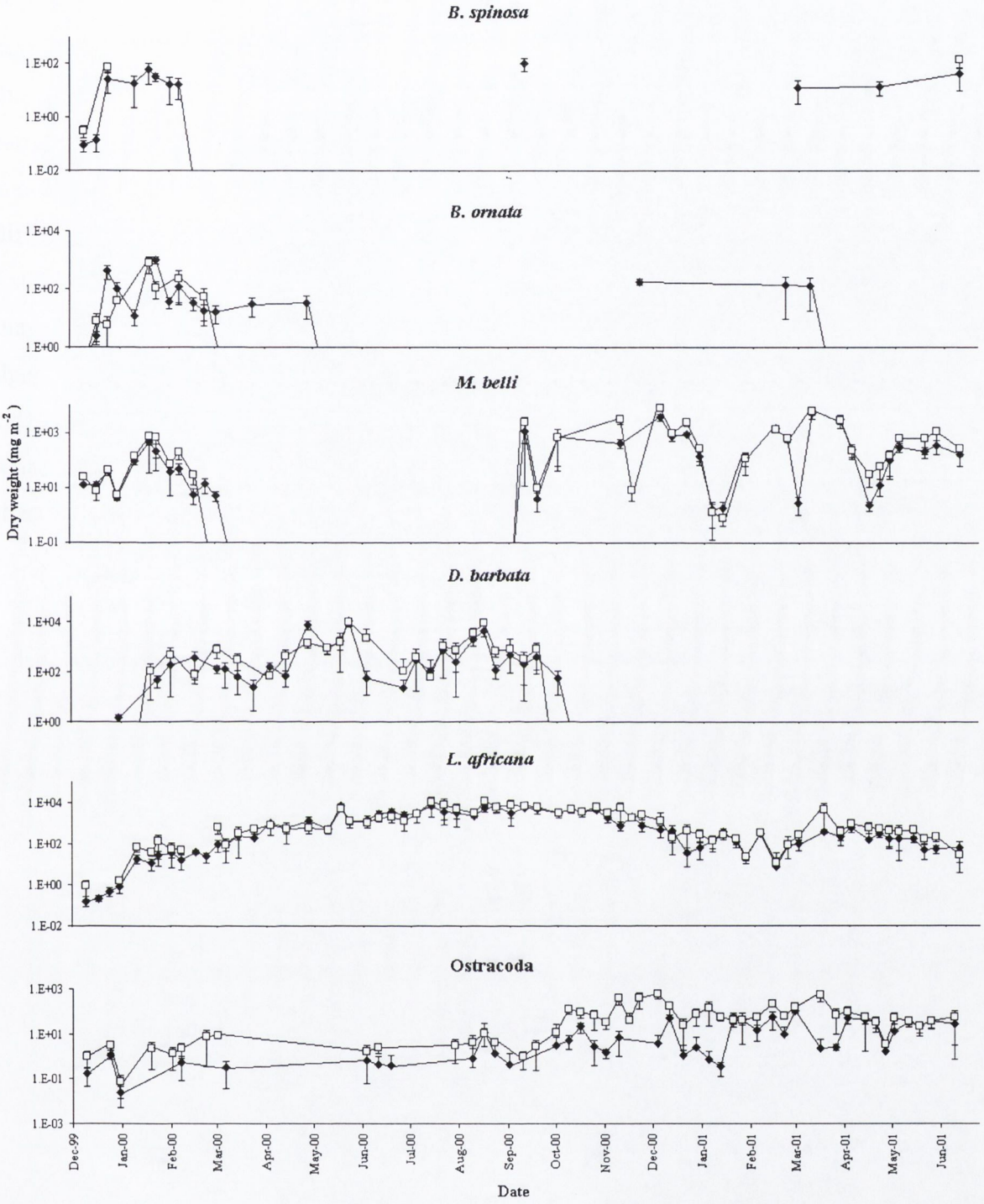

Figure 5.9 Weekly biomass in mg m^{-2} (± 95% CL) of the most common crustaceans on the north basin, estimated from samples taken using sweep net ◆ and tube □ sampling techniques, during the 1999-2000 and 2000-2001 wet seasons.

Weekly estimates for *B. spinosa* were consistently high in the middle basin and maximum recorded biomass during both seasons were considerably higher than those in the north basin (Table 5.9). In general, weekly estimates from both sweep net and tube samples correlated for *Branchinella* (Fig 5.10). *M. belli, L. africana* and ostracoda standing biomass varied considerably according to sample technique, with the greatest difference occurring at maximum biomass, between March and May 2000 (Table 5.9). Estimates for ostracoda, in particular, were much higher among tube samples and maximum recorded biomass for tube sample estimates was one order of magnitude higher than that from sweep net samples (Fig 5.10, Table 5.9). Greater correlation between estimates from both sampling techniques occurred during the 2000-2001 wet season. With the exception of *B. spinosa*, standing biomass for each species was, however, lower than the previous season (Fig. 5.10, Table 5.9).

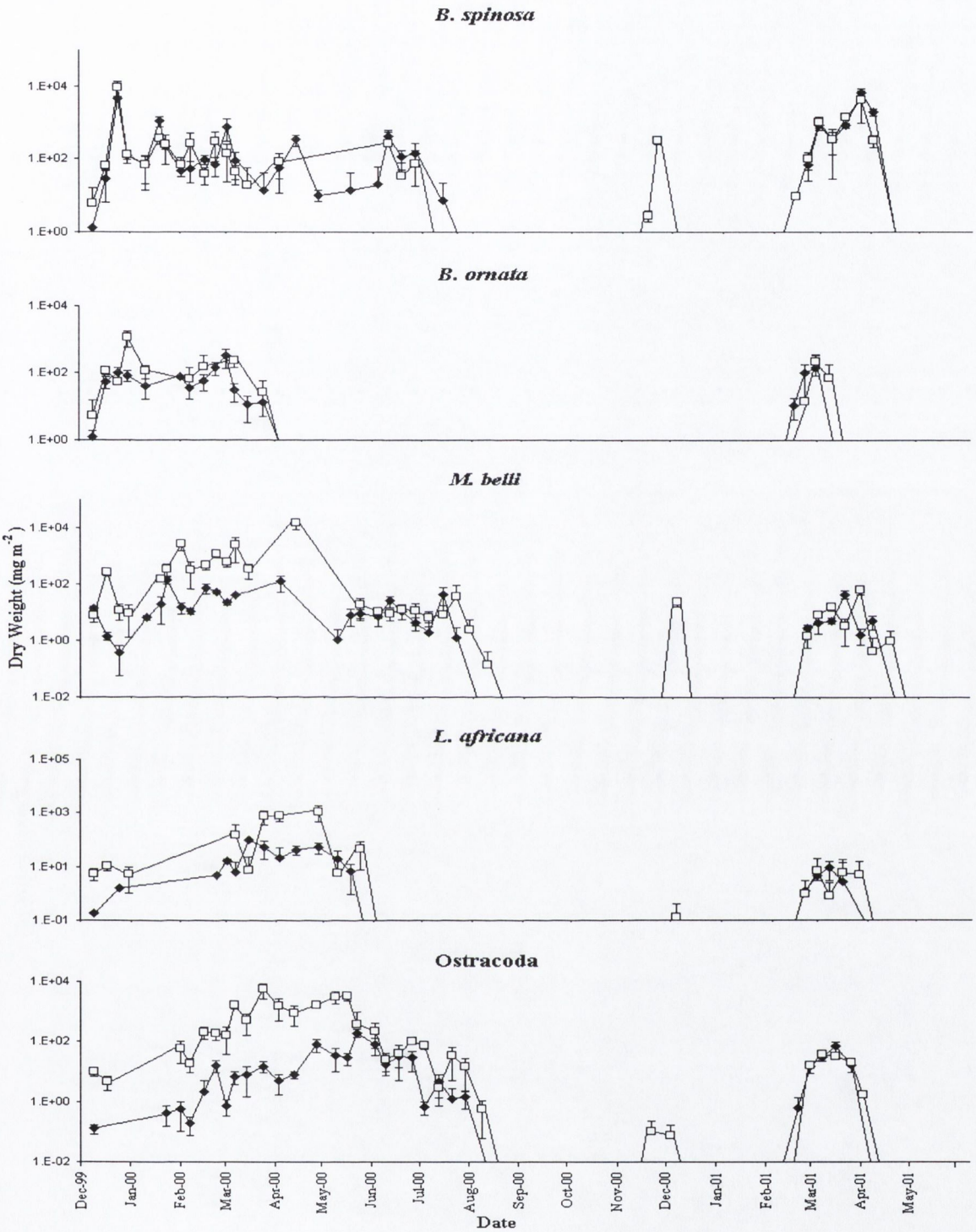

Figure 5.10 Weekly biomass in mg m^{-2} (± 95% CL) of the most common crustaceans on the middle basin estimated from samples taken using sweep net ◆and tube □ sampling techniques during the 1999-2000 and 2000-2001 wet seasons.

In the south basin, weekly estimates for *B. spinosa* were, again, consistently high during the 1999-2000 wet season, although recorded seasonal maxima were not as high as those in the middle basin (Fig 5.11 and Table 5.9). *B. ornata* biomass, in comparison, was much lower owing to its rarity. *M. belli* biomass estimates from tube samples were again much higher than those from sweep net samples and recorded maxima were separated by one order of magnitude (Table 5.9). Ostracod biomass was also higher among tube samples (Table 5.9). Biomass estimates during the 2000-2001 wet season were closely correlated in comparison with those from the previous season (Fig. 5.11, Table 5.9).

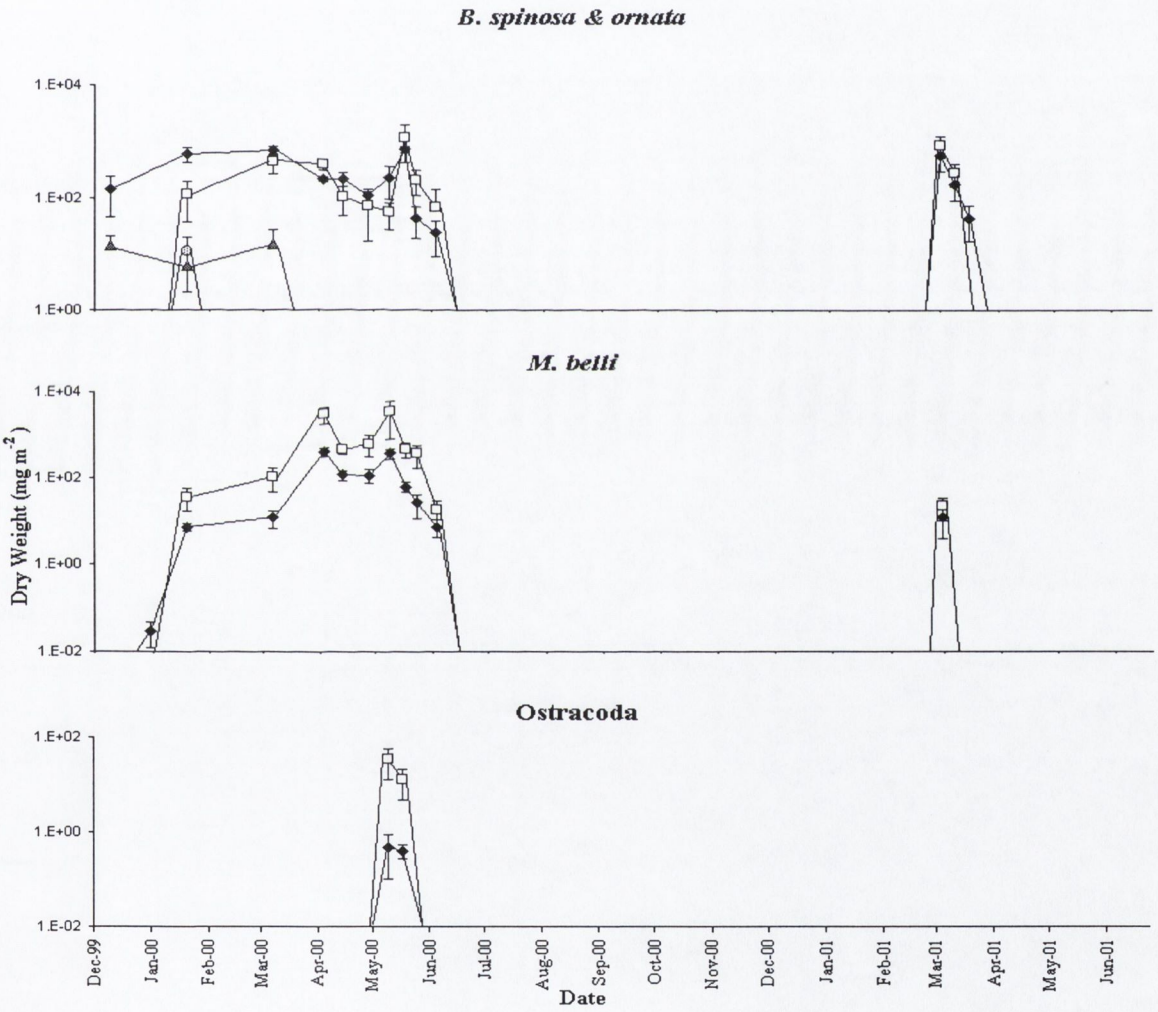

Figure 5.11 Weekly biomass in mg m^{-2} (± 95% CL) of the most common crustaceans on the south basin estimated from samples taken using sweep net ◆ and tube □ sampling techniques during the 1999-2000 and 2000-2001 wet seasons.

Table 5.9 Maximum biomass (mg m^{-2}) ± 95% CL estimates for the most common crustaceans in the north, middle and south basin, estimated from sweep net (sw) and tube (tb) samples during the 1999-2000 and 2000-2001 wet seasons.

		North		Middle		South	
Species	**Sample**	**99-00**	**00-01**	**99-00**	**00-01**	**99-00**	**00-01**
Br. spinosa	Sw	106 ± 55	42 ± 32	4597 ± 251	6677 ± 2238	725 ± 85	576 ± 279
	Tb	75 ± 26	141 ± 72	9248 ± 4038	4344 ± 3365	1198 ± 772	871 ± 351
Br. ornata	Sw	972 ± 253	178 ± 45	320 ± 190	140 ± 139	15 ± 12	0
	Tb	766 ± 449	0	1170 ± 584	212 ± 133	11 ± 9	0
M. belli	Sw	1137 ± 1125	4935 ± 1898	124 ± 72	45 ± 1	408 ± 87	12 ± 8
	Tb	2438 ± 2027	7615 ± 1704	15234 ± 6515	65 ± 22	3619 ± 2781	22 ± 12
D. barbata	Sw	10959 ± 3733	60 ± 48	0	0	0	0
	Tb	10447 ± 4375	0	0	0	0	0
L. africana	Sw	6904 ± 1958	4692 ± 1725	100 ± 38	9 ± 11	0	0
	Tb	11310 ± 3885	5868 ± 1340	1141 ± 667	6 ± 11	0	0
Ostracoda	Sw	12 ± 11	105 ± 129	198 ± 59	67 ± 27	49 ± 39	0
	Tb	10 ± 8	576 ± 218	5679 ± 2954	39 ± 10	34 ± 22	0
L. striatochonca	Sw	0 ± 0	0	0	0	0	0
	Tb	0 ± 0	0	0	0	0	0

5.3.4.2 Total seasonal biomass

Total weekly biomass and the proportion contributed by each species varied considerably during both wet seasons in each basin (Fig 5.12). In the north basin, total crustacean biomass was relatively low between December 1999 and the end of April 2000 and was dominated mainly by *M. belli* and *B. ornata.* During the winter months (April-September), large standing crops of *D. barbata* and *L. africana* increased total biomass and contributed to maxima recorded crustacean biomass estimates of 12 (sw) g m^{-2} in May and 20.5 g m^{-2} (tb) in August 2000 (Fig. 5.12); estimates were considerably higher from tube samples. *L. africana* contributed the majority of the total crustacean biomass in the 1999-2000 season (102.8 ± 42.7 g m^{-2} (sw); 126.6 ± 68.6 g m^{-2} (tb), Table 5.10). Large differences between the seasonal totals occurred as a result of tube sample estimates being considerably higher for *M. belli*, *L. africana*, and *D. barbata*. At the beginning of the 2000-2001 wet season, total biomass estimates were, generally, below 1 g m^{-2} (Fig. 5.12), and dominated by *M. belli* and ostracods. *L. africana* occasionally increased total crustacean biomass and contributed to recorded maxima of 5.1 (sw) and 6.14 g m^{-2} (tb) in mid March. During the 2000-2001 wet season, *L. africana* and *M. belli* comprised the majority of total biomass estimates (Table 5.10), with estimates from the tube 40 % higher than those from sweep net samples.

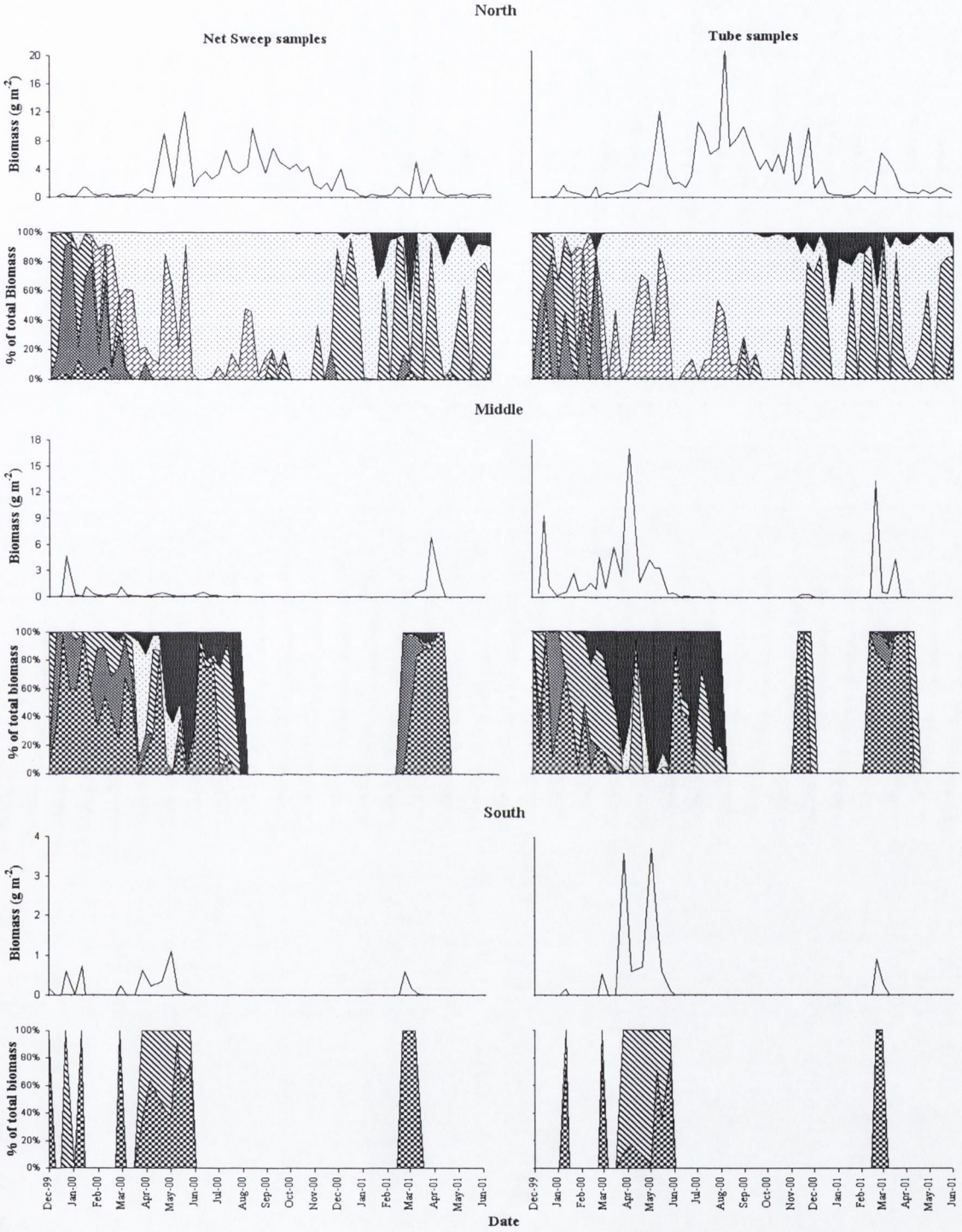

Figure 5.12 Total crustacean biomass (g m^{-2}) during the 1999-2000 and 2000-2001 wet seasons estimates from net sweep and tube sample techniques and the proportion of total crustacean biomass contributed by *B. spinosa* ▩ *B. ornata*, ▩ *M. belli*, ▩ *D. barbata*, ▩ *L. africana* □ and Ostracoda ▩ on the north, middle and south basins.

Table 5.10 Total seasonal dry weight (g m^{-2} ± 95 % CL) for each crustacean species taken from the north, middle and south basin of Sua pan, using net sweep (sw) and tube (tb) sample techniques, during the 1999-2000 and 2000-2001 wet seasons.

Species	Sample	North		Middle		South	
		'99-'00	'00-'01	'99-'00	'00-'01	'99-'00	'00-'01
B. Spinosa	Sw	0.3 ± 0.17	0.07 ± 0.05	9 ± 2.2	10 ± 3	3 ± 0.8	0.8 ± 0.4
	Tb	0.08 ± 0.03	0.14 ± 0.1	13 ± 6.4	6.2 ± 4	2.6 ± 1.4	1.2 ± 0.5
B. Ornata	Sw	2.7 ± 1.03	0.5 ± 0.3	1 ± 0.6	0.14 ± 0.1	0.035 ± 0.023	0
	Tb	1.2 ± 0.8	0	2.2 ± 1.2	0.07 ± 0.06	0.011 ± 0.01	0
M. belli	Sw	2.1 ± 1.5	18.2 ± 6.4	0.64 ± 0.26	0.06 ± 0.02	1.14 ± 0.29	0.012 ± 0.008
	Tb	4.4 ± 3.5	29.5 ± 10.6	24.2 ± 11	0.09 ± 0.03	8.9 ± 5.1	0.02 ± 0.012
D. barbata	Sw	31.8 ± 15.3	0.06 ± 0.05	0	0	0	0
	Tb	37 ± 19.8	0	0	0	0	0
L. africana	Sw	65.9 ± 24.6	25.6 ± 9	0.33 ± 0.15	0.02 ± 0.02	0	0
	Tb	83.9 ± 44.5	42.3 ± 21.8	2.9 ± 1.7	0.04 ± 0.02	0	0
Ostracoda	Sw	0.018 ± 0.026	0.64 ± 0.61	0.57 ± 0.27	0.13 ± 0.05	0.001 ± 0.0005	0
	Tb	0.057 ± 0.037	3.8 ± 2	20.5 ± 9.6	0.11 ± 0.03	0.05 ± 0.03	0
Total (g m^{-2})	Sw	102.8 ± 42.7	45 ± 16.4	11.9 ± 3.4	10.2 ± 3.3	4.2 ± 1.1	0.8 ± 0.4
	Tb	126.6 ± 68.6	75.7 ± 34.4	63 ± 29.8	6.5 ± 3.8	11.6 ± 6.5	1.2 ± 0.5

In the middle basin, *B. ornata* and, in particular, *B. spinosa* comprised large proportions of total crustacean biomass at the beginning of the 1999-2000 wet season (Fig. 5.12). *M. belli* and *L. Africana*, however, dominated standing biomass for the remainder of the season, with ostracods comprising large proportions when total biomass was low, particularly, among net sweep samples. Maximum standing biomass from tube samples (16.9 g m^{-2}), recorded in mid-April, comprised mostly *M. belli* (Fig. 5.12). Total standing biomass for the season was six times higher compared with the sweep net total owing to

higher *M. belli* and ostracoda biomass from tube samples (Fig. 5.12). During the floods of the 2000-2001 wet season, almost all of the total biomass comprised *B. spinosa*, with *M. belli* contributing more towards the end of the floods among tube samples. Maximum total biomass was recorded in March 2001 (6.8 g m^{-2} (sw); 13.3 g m^{-2} (tb)), and comprised mostly *M. belli*. The majority of the seasonal total, however, comprised *B. spinosa*.

During the 1999-2000 wet season, maximum weekly biomass in the south basin occurred in early May (1.1 g m^{-2} (sw) and 3.7 g m^{-2} (tb)). The overall lower standing biomass found in the south basin comprised almost entirely *B. spinosa* and *M. belli* (Fig. 5.12, Table 5.10). Total biomass estimates from tube samples were considerably higher than those from the net because of the higher *M. belli* and ostracoda abundance (Fig. 5.12). Indeed the seasonal total for tube samples was more than twice the sweep net total (Table 5.10). Sweep net total biomass for the season was, as before, dominated by *B. spinosa* (Table 5.10). Maximum total weekly biomass estimates for 2000-2001 of 0.59 (sw) and 0.89 g m^{-2} (tb) at the beginning of the flood period comprised entirely *B. spinosa* (Fig. 5.12). Seasonal total biomass estimates from tube samples were only slightly higher than those estimated from the sweep net (Table 5.10).

5.3.5 Crustacean production

5.3.5.1 Anostracan life history

Detailed length-frequency analyses between February 25th and April 20th, 2001, of *B. spinosa* and *B. ornata* tracked population growth through a middle basin flood period (Fig. 5.13). The first samples were taken on day three of the flood. Average individual length was 1.18 and 1.24 mm, respectively, for *B. spinosa* and *B. ornata*, after six days the populations reached, respective average lengths of 4.9 and 6.5 mm, and after fifteen 7.9 and 10.6 mm. *B. ornata* then disappeared from the samples, while average length of the *B. spinosa* population increased to 11.7, 15.8 and 18.9 mm at thirty, forty and forty eight days from the beginning of the flood. Average growth rate per individual of the *B. spinosa* population increased from 0.011 mg ind^{-1} day^{-1}, in the first week, to an average maximum rate of 0.073 mg ind^{-1} d^{-1}. Average growth rates for the *B. ornata* population during the first and second week were approximately double those of *B. spinosa* (0.022 – 0.032, compared with 0.016 mg ind^{-1} day^{-1} in the second week for *B. spinosa*). Approximately two weeks after hatching, *B. spinosa* females became ovigerous at 10.4 mm length. Mean number of eggs per female ranged from 2.9 on day fifteen of the flood (March 15th) to 23.9 eggs per female on the final sampling day, April 18th. At that time, the percentage of ovigerous females was > 90%. Egg counts in female egg sacs ranged from 8 to 171 and, generally, more numerous in larger females. There were some exceptionally large and fast growing individuals of both species early in the flood period, reaching maturity considerably earlier than the average individual.

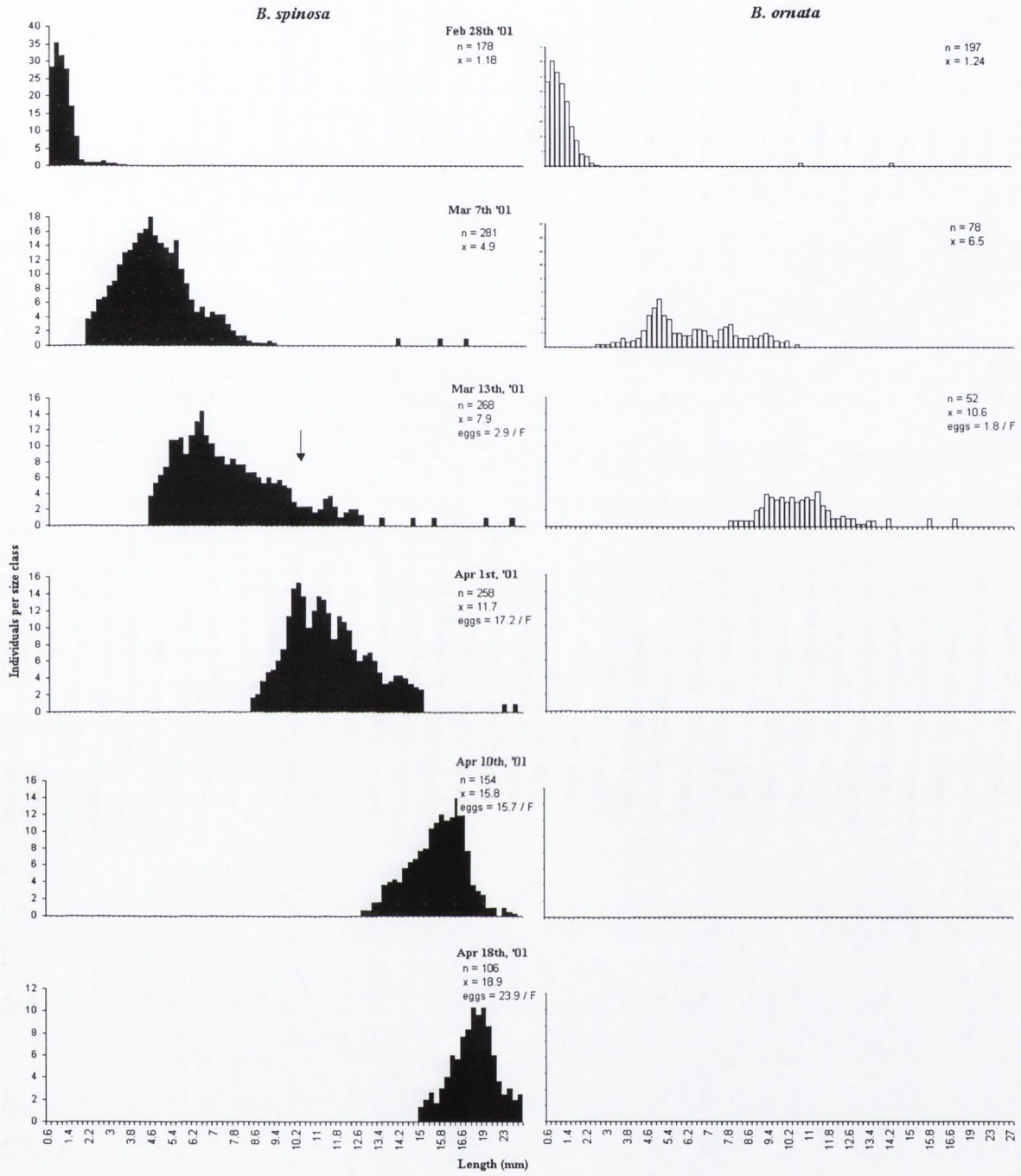

Figure 5.13 Length-frequency histograms of a single cohort of *B. spinosa* and *B. ornata* in weekly samples from the middle basin during the 2001 flood period (beginning 25th February and ending April 20th, 2001). Size class data was smoothed by three point running average. *n* equals number of individuals measured each week and *x*, the mean size class of individuals in the cohort. Mean eggs per female in the population is also given, and the arrow indicates the length at which *B. spinosa* females first produce eggs.

5.3.5.2 Anostracan growth and P:B ratios

Weekly size-frequency distribution analyses of *B. spinosa* and *B. ornata* populations in all three basins identified multiple cohorts in each season. Population biomass varied with basin and species (Fig. 5.14). In the north basin, a single cohort of each species of anostracan emerged at the beginning of the flood period and grew rapidly. Mean individual *B. spinosa* dry weight increased from 0.003 to 2.2 mg over the period of two months at an average growth rate of 0.037 mg ind^{-1} day^{-1}, while the average dry weight of *B. ornata* increased from 0.01 to 2.48 mg over a similar period at an average growth rate of 0.03 mg ind^{-1} d^{-1}. When species became very rare during the 2000-2001 wet season, it was difficult to identify cohorts.

Two cohorts of *B. spinosa* were identified during the 1999-2000 flood period. The second emerged in early February 2000, soon after the majority of females from the first cohort reached maturity. Populations of both increased in biomass at slightly different rates (averaged 0.02 mg ind^{-1} d^{-1} in the first cohort and 0.03 mg ind^{-1} d^{-1} in the second). A similar rate of 0.023 mg ind^{-1} d^{-1} was calculated for individuals in a cohort of *B. ornata* that also emerged at the beginning of the season. Average individual dry weight in the *B. spinosa* population then decreased dramatically towards the end of the flood period as the population comprised mostly small individuals. Population growth rates increased during the 2000-2001 wet season. B. spinosa individuals grew at an average rate of 0.035 mg ind^{-1} d^{-1}, while *B. ornata* individuals grew at an average 0.028 before it disappeared (Fig. 5.14).

In the south basin, two cohorts of *B. spinosa* were also identified during the 1999-2000 flood period. The average increase in individual biomass of the first cohort was considerably lower (0.047 to 2.4 mg) than in the other basins. Average growth rate was 0.013 mg ind^{-1} d^{-1}. During the second cohort, identified in April 2000, average individual biomass increased from 1.14 to 3 mg, an average rate of 0.05 mg ind^{-1} d^{-1}. As in the middle basin, average individual weight decreased rapidly towards the end of the flood period as the lake dried up. A small cohort of *B. ornata* was also identified at the beginning of the flood period in which individuals grew at an average daily rate of 0.03

mg ind^{-1} over a short time (Fig. 5.14). *B. spinosa* emerged again during the short flood of the 2000-2001 wet season but was present in the samples for only two weeks. Low densities made estimates of population biomass unreliable.

Estimated weekly P:B ratios, calculated from the identifiable cohorts (above) varied among basins. Mean P:B ratios calculated for *B. spinosa* in the north and middle basin at the beginning of the 1999-2000 flood period were 0.75 (ranging from 0.31 to 2.35) and 0.9 (ranging from 0.04 to 3.19), respectively. P:B ratios during the 2000-2001 flood period, ranged from 0.27 to 1 and averaged 0.65 in the middle basin. In the south basin P:B ratios ranged from 0.07 to 3 and averaged 0.93 in the 1999-2000 wet season. Weekly P:B values for *B. ornata* in the north basin ranged from 0.2 to 3.3 with an average of 0.67.

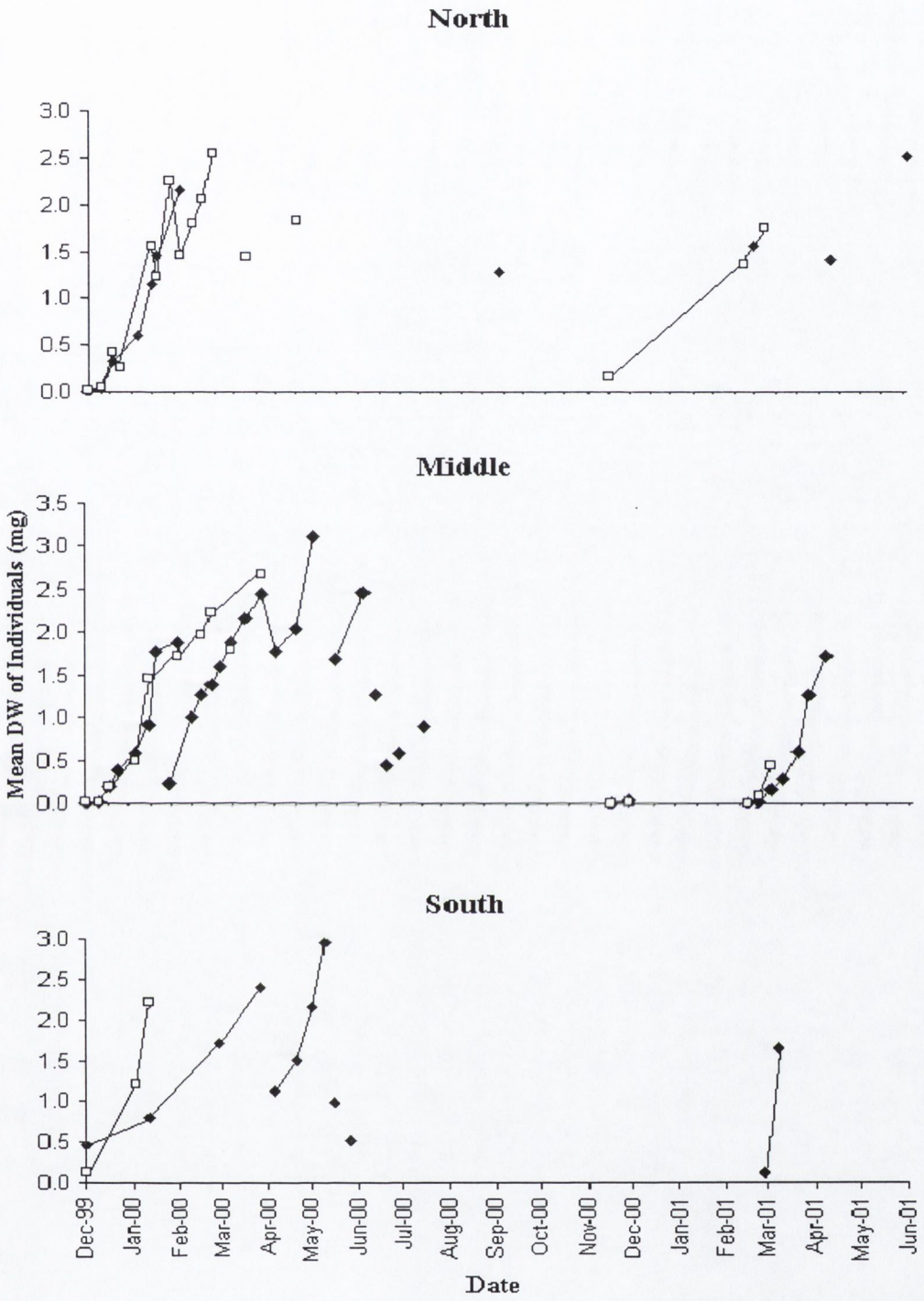

Figure 5.14 Growth of *B. spinosa* ◆ and *B. ornata* □ , among different cohorts that emerged during the 1999-2000 and 2000-2001 wet seasons on three basin lakes. Those values not linked with lines represent samples that could not be used in 'growth increment summation' estimates. P:B ratios were used to convert biomass on these dates.

5.3.5.3 Crustacean production

Weekly total crustacean production fluctuated considerably among the basins and seasons, as did the proportion of the totals contributed by each species (Fig. 5.15). Productivity at the beginning of the 1999-2000 wet season was low in the north basin, comprising mostly *M. belli* with occasional peaks of *B. ornata*. The emergence of *D. barbata* increased weekly totals in April and May, and a gradual increase in *L. africana* productivity during the winter months contributed to relatively high total production (~ 2 g m^{-2} wk^{-1}) for much of the winter period (June to September 2000). Occasional peaks in *D. barbata* and *L. africana* production increased weekly totals even higher as summer approached and temperatures increased. In September 2000, a large increase in *M. belli* productivity contributed to recorded seasonal maxima of 4.8 (sw) and 7.7 (tb) g m^{-2} wk^{-1}. *M. belli*, again, accounted for a peak in total production of 8.3 (sw) and 16.7 g m^{-2} (tb), in December 2000. Total productivity then decreased to below 500 mg m^{-2} wk^{-1} for the month of January. With the onset of rains, and more flooding in February 2001, there was an increase in *M. belli* production, contributing to recorded seasonal maxima of 10.4 (sw) and 12.8 (tb) mg m^{-2} in March 2001. Total production remained relatively low (< 1 g m^{-2} wk^{-1}) for the winter months of 2001, apart from occasional peaks in *M. belli* production.

Considerably lower estimates of weekly crustacean production were obtained from sweep net compared with tube samples collected from the middle basin (Fig 5.15). During the 1999-2000 wet season much of the weekly totals comprised *M. belli*, and *B. spinosa*, with ostracoda contributing the majority of total estimates later in the season. Estimates from net sweep samples remained below 0.5 g m^{-2} wk^{-1}, with occasional peaks > 0.5 g m^{-2} wk^{-1} in late January, mid April and late May 2001. These peaks coincided with increases in, respectively, *M. belli* and *B. spinosa*, *M. belli*, and ostracod production. Weekly estimates from tube samples were, in general, two orders of magnitude higher with recorded maxima in April 2001 of 61.5 g m^{-2} wk^{-1}. This comprised almost entirely ostracod and *M. belli* production. Total production estimates were, however, higher among sweep net samples than tube samples during the 2000-2001 wet season (Fig. 5.15). *B. spinosa* and *M. belli* contributed to maximum recorded weekly production of 1.9 (sw) and 0.2 g m^{-2} wk^{-1} (tb) in April 2001.

During the 1999-2000 wet season, weekly production estimates in the south basin were, again, higher among tube samples compared with the sweep net samples (Fig. 5.15). Relatively high *M. belli* and *B. spinosa* productivity contributed to a recorded seasonal maximum of 1.5 g m^{-2} wk^{-1} in April 2000 among sweep net sample estimates. The recorded seasonal maximum among weekly tube sample estimates was an order of magnitude higher, reaching 13.2 g m^{-2} wk^{-1}, in May 2000. During the 2000-2001 flood, production was considerably lower and the recorded seasonal maxima were 0.36 (sw) and 0.08 g m^{-2} wk^{-1} (tb), with *M. belli* and *B. spinosa*, again, comprising the majority of the total.

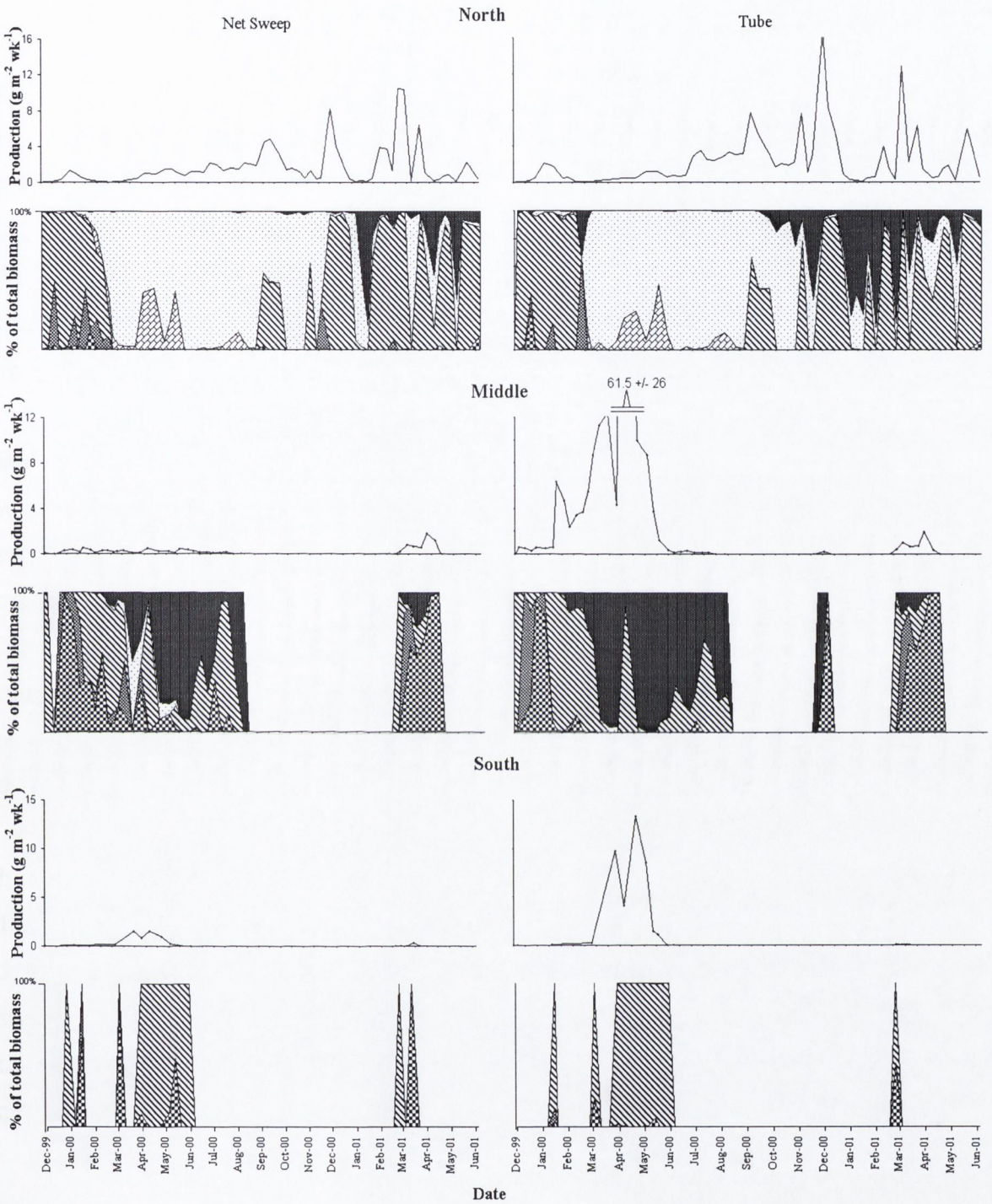

Figure 5.15 Total production in g m^{-2} wk^{-1} and proportions contributed by *B. spinosa* ▩, *B. ornata* ▩, *M. belli* ▩, *D. barbata* ▩, *L. africana* ▩ and ostracods ▩ on the north, middle and south basins of Sua pan, during the 1999-2000 and 2000-2001 wet seasons.

5.3.5.4 Total seasonal production

Total crustacean production during the 1999-2000 season was 38.7 g m^{-2} for sweep net estimates and 52.05 g m^{-2} for tube sample estimates, owing to higher production totals for *L. africana* and *M. belli* from tube samples. During the 2000-2001 wet season total production by *M. belli* was by far the highest among crustacean totals, with total production estimated from tube samples higher than the sweep net samples. *L. africana* production was less than half that of the previous season, while that of ostracods was higher. Total crustacean production estimates for tube samples was, overall, 30% higher than sweep net samples during the 2000-2001 wet season: 68.14 (sw) and 98 g m^{-2} (tb).

In the middle basin, *M. belli* was the most productive crustacean during the 1999-2000 wet season, with estimates from tube samples an order of magnitude higher than from the sweep net (Table 5.11). Ostracod total production was also far greater from tube samples, contributing to production estimates of 5.86 (sw) and 152.3 g m^{-2} (tb) during the 1999-2000 season. Total production of *B. spinosa* was higher compared with estimates from the north basin. During the 2000-2001 wet season, *B. spinosa* production was an order of magnitude higher than the seasonal total for all other species. Total crustacean production estimates for the 2000-2001 wet season were 5.31 (sw) and 5.34 g m^{-2} (tb).

In the south basin, *M. belli* was, again, by far the most productive crustacean during the 1999-2000 wet season, with large differences between sample technique estimates (Table 5.11). Crustacean totals for the 1999-2000 flood period could not be established as samples were only taken during a total of eleven weeks, out of a total flood period of ten months. Crustacean biomass totals for these eleven weeks were 5.6 (sw) and 38.55 (tb), and comprised almost entirely *M. belli* production. In comparison, *M. belli* production was two to three orders of magnitude lower during the 2000-2001 wet season. Total crustacean production was an estimated 0.38 (sw) and 0.08 g m^{-2} (tb) for that season and comprised mostly *B. spinosa* production.

Table 5.11 Total seasonal production in g m^{-2} (± 95% CL) for each crustacean species, taken from the north, middle and south basin (11 weeks) of Sua pan, using sweep net (sw) and tube (tb) sample techniques during the 1999-2000 and 2000-2001 wet seasons.

Species	Sample	North		Middle		South	
		'99-'00	'00-'01	'99-'00	'00-'01	'99-'00	'00-'01
Br. spinosa	sw	0.17 ± 0.11	0.04 ± 0.03	1.37 ± 0.39	4.28 ± 1.23	0.59 ± 0.16	0.36 ± 0.2
	tb	0.05 ± 0.02	0.03 ± 0.02	1.75 ± 0.61	4.11 ± 1.57	0.32 ± 0.14	0.04 ± 0.02
Br. ornata	sw	0.41 ± 0.17	0.33 ± 0.19	0.32 ± 0.2	0.37 ± 0.33	0.03 ± 0.02	0
	tb	0.42 ± 0.21	0	0.43 ± 0.37	0.48 ± 0.28	0.004 ± 0.002	0
M. belli	sw	8 ± 5.8	57.2 ± 19.5	2.36 ± 0.96	0.29 ± 0.1	5 ± 1.32	0.025 ± 0.017
	tb	14.2 ± 11.3	72.9 ± 27.3	86.7 ± 39.52	0.46 ± 0.17	38.2 ± 22.83	0.046 ± 0.026
D. barbata	sw	2.36 ± 1.1	0.002 ± 0.001	0	0	0	0
	tb	2.42 ± 1.31	0	0	0	0	0
L. africana	sw	27.7 ± 10.6	8.85 ± 3.1	0.16 ± 0.07	0.006 ± 0.006	0	0
	tb	34.8 ± 18.4	14.7 ± 7.5	1.14 ± 0.6	0.007 ± 0.017	0	0
Ostracoda	sw	0.041 ± 0.059	1.7 ± 1.6	1.64 ± 0.75	0.37 ± 0.14	0.002 ± 0.001	0
	tb	0.14 ± 0.1	9.7 ± 5.2	62.3 ± 29.65	0.28 ± 0.07	0.013 ± 0.008	0
L. striatoch	sw	0 ± 0	0	0	0	0	0
	tb	0 ± 0	0	0	0	0	0
Total (g m^{-2})	sw	38.7 ± 17.9	68.14 ± 24.4	5.86 ± 2.4	5.31 ± 1.8	5.6 ± 1.5	0.38 ± 0.2
	tb	52.05 ± 31.4	98 ± 33.8	152.3 ± 70.75	5.34 ± 2.1	38.55 ± 23	0.08 ± 0.05

5.4 Discussion

5.4.1 Community composition and species distribution

Although crustacean community composition in the north basin of Makgadikgadi is generally similar to that recorded decades ago (Eccles, undated), there does appear to be some differences. Most notable is the absence of the anostracan *Streptocephalus proboscideus*, found in the north basin by the expedition team of 1957 and again in the late 1990s by Brendonck & Riddoch (1997). When Brendonck & Riddoch (1997) sampled the north basin, *B. ornata* was the only other anostracan present in the north basin, while *B. spinosa* was only recorded in adjacent pans. Salinity and pH levels at the time were similar to those taken during the early part of the 1999-2000 flood period (5200 to 21300 μs cm^{-1}, with pH 8.9 to 9.5). While species richness occasionally is much higher in some episodic pools, the anostracan community appears unstable and species not adapted to the hydrological and chemical regimes of the water body become extinct (Hamer & Rayner, 1996). *S. proboscideus* could, therefore, be a vagrant species in this unstable habitat, although its absence during this study does indicate a possible long-term change in anostracan community structure. *Mesocyclops leuckarti* and the ostracod *Cypridopsis newtoni* were also absent during this study, although their very rare status reported by Eccles suggests they were vagrant species. *M. belli*, however, may have been misidentified as *M. macrocopa* by the expedition team in 1957, considering its description is very similar to that of *M. belli* (Seaman *et al.*, 1999). Its unpredictable ephemeral nature (Chapter 2), combined with a unique chemistry among southern African saline lakes (Chapter 3) may explain Sua pans unique crustacean community. Some of the most predominant species on Sua pan, *B. spinosa* and *L. africana*, are found nowhere else in southern Africa (Brendonck & Riddoch, 1997; Rayner & Heeg 1994), while others, *M. belli* and *L. tudoranceai* have been found only in a few temporary waters in Namibia (Day, 1990; Martens *et al.*, 1996).

Variation in species richness, both between and among all three basins during the two wet seasons, could be related to a number of physical and biological factors that control species distribution. The most important of these in shallow saline lakes is probably salinity, which is negatively correlated with species richness (e.g. Hammer, 1986; Williams DD, 1987; Green, 1993; Williams *et al.*, 1990). A reduction in species richness concurrent with increased salinity was most noticeable along a north to south gradient. Eleven species occurred in the north, five occurred in the middle and four in the south basin (Fig. 5.3, 5.4 & 5.5). Those species associated with low saline conditions, *M. transvaalensis*, *D. barbata*, *L. striatochonca* and the ostracods *P. aldabrae* and *Potamocypris*, occurred in the north basin only at the beginning of the 1999-2000 wet season, when the water was least saline (Chapter 3). In comparison, *B. spinosa*, *M. belli*, and *L. tudoranceai* occurred in all three basins across a wide salinity range of 320 μS cm^{-1} and >50 mS cm^{-1} and between pH 8.5 and 10. *B. spinosa* and *M. belli* occurred at maximum conductivities of 112 and 65 mS cm^{-1} respectively, while *L. tudoranceai* was not found at salinities >70 mS cm^{-1}. *B. ornata* disappeared quickly from both the middle and south basins coinciding with increases of salinities >20 mS cm^{-1} (Fig. 5.2 & 5.3). *L. africana* was found in the middle basin up to salinities of 38 mS cm^{-1}, but not at the higher salinities found in the south basin (Chapter 3). Maximum salinity tolerances for *M. belli* and *L. africana*, therefore, appear higher on Sua pan compared with alkaline lakes in East Africa and Ethiopia. No *M. belli* have been recorded in East African soda lakes with salinities >21 mS cm^{-1} and *L. africana* disappear from lakes between 21 and 25 mS cm^{-1} (Vareschi & Vareschi, 1984; Melack, 1988; Green, 1993). Higher proportions of lethal ions, such as fluoride, in the chemical composition of East African saline lakes may result in lower salinity tolerances of species in those lakes compared with Sua pan. Higher pH or HCO_3^- / CO_3^{2-} levels in East African lakes compared with Sua pan may also influence crustacean salinity tolerance.

Among the basins of the Makgadikgadi, species richness changed over time. Reductions in species numbers in the middle and south basins appeared to result from increasing salinities (discussed for each species above), associated with a disappearance of *B. ornata* and *L. africana* from the middle basin and *B. ornata* from the south basin during the

1999-2000 wet season (Fig. 5.3 & 5.4). A temporal decrease in species richness was, however, most noticeable in the north basin, where the number of species ranged from 11 to 3 during the flood period and where factors other than salinity may have influenced species numbers. All eleven species occurred in the north basin during the beginning of the 1999-2000 wet season when salinity was at its lowest (Chapter 3). The occasional appearance and subsequent rapid disappearance of rare species like *Metadiaptomus transvaalensis*, and the ostracods *Plesiocypridopsis aldabrae*, and *Potamocypris* suggest they may have been opportunistic vagrant species from surrounding pans and with low salinity tolerance. Among the common species, the most noticeable disappearance of a freshwater species was that of the conchostraca *L. striatochonca.* Its rapid disappearance in March 2000 (Fig. 5.2) may have occurred as a result of predation. As a result of their evolutionary isolation from vertebrate predators in temporary waters, many euphyllopoda species and other large planktonic crustacean species are highly susceptible to predation by planktivorous fish (Hammer, 1986; Allanson *et al.*, 1990; Day *et al.*, 1999). The unusual presence of *Tilapia* and, in particular, 'Barbel' fish (Cyprinidae) in the north basin, during the exceptional floods, may have caused local extinctions of *L. striatochonca* and other large crustaceans, as classically described by Brooks & Dodson (1965). Indeed, the unusual disappearance of both *Branchinella* species in the north basin, in mid February (*B. spinosa*) and early May 2000 (*B. ornata*), underscores the likelihood of phyllopod species exclusion by fish predation. A number of fish were caught during the study period and their gut contents did, in fact, reveal a diet that included large crustaceans, mainly conchostracans. Invertebrate predation by aquatic insects like *Anisops* may have exacerbated predatory exclusion (Brendonck & Riddoch 1997). Co-existence of large crustaceans and planktivorous fish elsewhere in southern Africa has been explained by high levels of turbidity, providing a visual refuge for crustaceans (Hart 1986, Jarvis 1986). As lake levels decreased on the north basin, reductions in the Barbel population were evident and *Branchinella* re-immerged or increased from undetectable numbers during the 2000-2001 wet season. Salinity and pH may have, however, been too high for the re-emmergence of *L. striatochonca* during 2001. Large reductions in anostracan populations also occurred in the middle and south basins. At high densities, Greater flamingo have a considerable impact on invertebrate

abundance (Arengo & Baldassare, 1995; Comin & Hernandez, 1997; Glassom & Branch, 1997*a*). Glassom & Branch (1997*a*) estimated that the presence of Greater flamingo in two Namibian coastal lagoons reduced macro-invertebrate densities by up to a third. Zweers *et al.* (1995), in a study of size preference in the diet, found that Greater flamingo filter efficiency was highest with prey length of between 2 and 4 mm. During their lifespan, anostracans are among the few crustacean species that fall into this size category on Sua pan. A high proportion of anostracans were found in opportunistically collected crop samples of Greater flamingo (Chapter 6).

Successions of anamopoda species in the north basin may also have been the result of biological interactions. Apart from its exclusion from the south basin seemingly driven by extreme salinities (>50000 μS cm^{-1}), *M. belli* was only ever absent from Sua pan during a period of crustacean community domination by the larger *D. barbata*, between March and September 2000 (Fig. 5.2). Successions among anomopoda species have been associated with the nature and availability of food resources in other southern Africa lake systems (e.g. Kalk, 1979*a*; Jarvis, 1987). In such cases, large *Daphina* species dominate during periods when small edible algae are abundant and following the depletion of this food source and subsequent dominance of inedible blue-green algae, owing to changes in temperature, nutrients and salinity, *Daphnia* populations decrease and conditions become more favourable for small bodied omnivorous anomopoda, like *Moina* and *Ceriodaphnia*. Hart (1986; 1988) argues that seasonal appearance and disappearance of anamopoda species depends upon turbidity levels, which influence species-specific feeding rates and therefore competitive ability. Seasonal changes in temperature can have additional influences on these successions, and abundance of *D. barbata* is regularly associated with the cool season (e.g. Kalk, 1979*a*; Saint-Jean, 1983, Hart, 1986). While the possibility of salinity intolerance cannot be discounted, the disappearance of *D. barbata* from the north basin coincided with a reduction in small green algae and chroococcus during September 2000 (Chapter 4) and an increase in water temperature (Chapter 2).

5.4.2 Crustacean abundance and sampling technique

When estimating crustacean abundance, the advantages and disadvantages of using net sweep and tube sampling techniques in very shallow and highly variable lake levels have been highlighted in this study. In general, sampling crustaceans with the tube selected for much higher abundance estimates among the smaller, more abundant crustaceans, especially in shallower waters when densities were very high. Sweep net sampling was less efficient at catching zoobenthic crustaceans but more efficient at catching the larger phyllopoda at low densities.

Of all the crustacean species, phyllopoda numbers were generally lowest (Fig. 5.2, 5.3, 5.4, 5.5) owing to their larger size, longer generation time and higher susceptibility to predation by fish and Greater flamingo. Between the *Branchinella* species, *B. ornata* was more abundant at lower salinities in the north basin (Fig. 5.2), while a wider tolerance to salinity contributed to the dominance of *B. spinosa* in the middle and south basins. Tube sampling gave higher abundance estimates at the beginning of the flood periods owing to its higher catch efficiency of smaller individuals at higher concentrations (Fig. 5.2, 5.3, 5,4). Catch efficiencies decreased dramatically, however, at low densities, particularly among *Branchinella*, resulting in an absence of tube sample abundance estimates for much of the flood period in the north basin (Fig. 5.2) and in significantly higher overall abundance estimates from sweep net samples for *B. ornata* (Table 5.5). In general, sweep net sampling was the more consistent method for sampling larger, less numerous anostracans.

Smaller bodied anamopoda and copepoda were consistently the most numerous crustaceans on Sua pan (Table 5.3), with mean and maximum density estimates higher than those recorded from other saline lakes in Africa (e.g. Berry, 1972; Allanson *et al.*, 1990; Vareschi & Vareschi, 1984; Mepham, 1987). A large difference in seasonal mean abundance estimates from the different sampling techniques was evident, particularly, in the shallower waters of the middle and south basins (Fig. 5.5). This may have resulted from net blockage and considerable sample loss as a result of backflow when using the

sweep net technique, particularly in conditions of high silt turbidity and phytoplankton densities. Sweep net estimates of abundance in the deep waters of the north may have been biased owing to the vertical aggregations of small crustaceans near the lake surface and subsequent overestimates of areal abundance. The tube, in contrast, sampled the entire water column (or the majority of it when the lake was deepest in the north basin). The greatest difference between sampling techniques was evident among weekly abundance estimates of ostracoda (Fig. 5.5, Table 5.4). Zoobenthos abundance is, generally, linked to lake level fluctuations, which influence food and habitat availability (Hart, 1985; Cantrell, 1988). Being predominantly benthic (Day *et al.*, 2001), ostracods are, therefore, influenced by water depth and level and abundance is, therefore, likely to alter as a result of these changes. This was most evident in the north basin, where ostracod abundance was considerably lower at the beginning of the flood period, owing perhaps to low temperatures and oxygen levels on the benthos in the deepest waters (Hart 1985), while abundance increased when the lake decreased in depth. Higher abundance estimates among tube samples were, particularly, evident at the beginning of the flood period in both the north and middle basins, when floods were at their deepest (Fig. 5.2, 5.3). This large difference was the result of an inability to sample the entire water column in deep waters with the net, while tube sampling was more likely to have included more animals from the benthic surface and just above it. This explains why there was a closer correlation between sample estimates towards the end of the flood periods when the lake was shallow and the entire water column was sampled by the sweep net.

5.4.3 Biomass and production

5.4.3.1 Length-Weight relationships

The length weight relationships for *Branchinella, M. belli, L. africana* and ostracoda were statistically sound, with significant mean regressions and low residual mean squares (Table 5.8, Fig. 5.8). Each had a slope *b* that was in agreement with other studies on many freshwater zooplankton (Bottrell *et al.*, 1976; McCauley, 1984; Mengestou & Fernando, 1991). Slope *b* for *Branchinella* (2.36) was similar to those of anamopoda and copepods reflecting similar length-weight relationships among anostracans. In comparison to other fairy shrimp species, it was less than the slope *b* of a length-dry weight relationship for a similar sized anostracan species, *Parartemia zeitziana* (2.63) found by Marchant & Williams (1977) from populations in Australian shallow saline lakes. It was also considerably less than the slope of 3.16 found by Hildrew (1985) for the temporary rainpool anostracan *Streptocephalus vitreus*, in Kenya. A decline of the dry weight of *Branchinella* individuals from their emergence from the egg to roughly midway through the early developing stages (from 0.4 to 1mm) suggests utilization of food reserves during the first few days of life (Hart *et al.* 1995). The rate of increase in dry weight with length (slope *b*) was highest among the ostracods, although a small size range is known to affect the slope of small crustaceans in this way (e.g. Bottrell *et al.* 1976). The length-weight relationship (from Bottrell *et al.*, 1976) used to convert *D. barbata* mean population lengths into weekly biomass estimates contained a slightly higher slope *b* than those calculated for the other species by linear regression. Biomass estimates for this species might, therefore, be slightly over-estimated.

5.4.3.2 Crustacean biomass

The single most important determinant of zooplankton abundance on shallow saline lakes elsewhere in Africa, subject to large water level fluctuations and even dry periods, is water budget (e.g. Kalk, 1979*a*,*b*; Saint-Jean, 1983; Gras & Saint-Jean, 1983; Rzoska, 1984). Water budget, in turn, influences other controlling factors like salinity, turbidity and food availability from river inflow. This was evident on Sua pan where zooplankton

biomass, like community composition (discussed above) varied considerably among basins owing to different hydrological regimes, which controlled, most importantly, flood period and salinity, but also temperature, turbidity and food levels (Fig. 5.9, Table, 5.9). When the mean areal crustacean biomass estimates (g m^{-2}) for the flood periods in each basin were compared, the highest crustacean biomass estimates, 0.33 (sw) and 0.41 g m^{-2} (tb), occurred in the north basin during the 1999-2000 wet season. This was predominantly a result of large standing crops of the species *L. africana* and *D. barbata* during the winter period of that season. Relatively deep turbid waters, (Chapter 2), with low salinity, high nutrient levels (Chapter 3), and a highly productive phytoplankton community (Chapter 4) may have contributed to conditions of high food availability, sufficient refuge from predators and optimal conditions for high standing biomass. Crustacean standing biomass was lowest in the south basin, with an average standing biomass of 0.04 g m^{-2} for both sample techniques during the brief flood period of the 2000-2001 wet season. A very short flood period and the harsh physical and chemical conditions (Chapter 2, 4) contributing to low crustacean biomass is consistent with studies elsewhere on temporary waters (e.g. Rzoska, 1958, 1984). Lower areal standing biomass on the middle and south basin may also be owing to their shallow nature compared with the north basin. Large flocks of Greater flamingo also consistently favoured both basins and predation by the birds may, therefore, have reduced the crustacean standing crop considerably (Chapter 6). When compared with average crustacean biomass estimates from other shallow saline lakes in Africa, estimates from Sua pan were very similar to those from Lake Chad, which ranged from 0.18 to 0.4 g m^{-2} over a two year period, 1972-73 (Leveque & Saint-Jean, 1983) and the range of variation (20-400 fold) in zooplankton biomass was very similar to that found in Lake Chilwa (Kalk, 1979*a*,*b*). While total areal biomass estimates from saline lakes in tropical East Africa were higher (e.g. L. Awasa, 0.9 g m^{-2} (Mengestou & Fernando, 1991), L. George, 0.8 g m^{-2} (Burgis, 1974) and L. Nakuru, about 2.1 g m^{-2} (Vareschi & Jacobs, 1984), Sua pans waters were considerably shallower. Indeed, volumetric biomass estimates on Sua (0.4 – 0.5 g m^{-3}) are higher than L. George and L. Chad and an order of magnitude higher than that estimated from L. Awasa (Burgis, 1974; Leveque & Saint-Jean, 1983; Mengestou & Fernando, 1991).

There was very little correlation between zooplankton standing biomass and that of total phytoplankton (Chapter 4). Much of the phytoplankton biomass comprised blue-green algae of perhaps low edibility, which could restrict transfer of biomass between trophic groups. There does, however, appear to be some correlation between zooplankton standing biomass and the standing crop of the small green algae and *Chroococcus*, particularly in respect to *M. belli, D. barbata* and *L. africana* standing biomass (Chapter 4). The ratio of phytoplankton standing biomass to crustacean standing biomass (P/Z ratio) gives a rough measure of the energy transfer between the two communities (Brylinsky & Mann, 1973; McCauley & Kalff, 1981). In high latitude lakes, large fluctuations in the P/Z ratio are common (Sprules *et al.*, 1983). This is indeed true for ratios from all the basins owing to, generally, very low ratios at the beginning of the season and very high ratios at the end of it (Table 5.12).

Table 5.12 Phytoplankton – Zooplankton standing biomass ratios (g m^{-2}) in the north, middle and south basins, during the 1999-2000 and 2000-2001 wet seasons.

Basin	Season	Sample	Seasonal range	Seasonal Mean ratio
North	1999-2001	sweep net	0.002 – 41	4
		Tube	0.001 – 24	2
Middle	1999-2000	sweep net	0.001 – 167	12
		Tube	0.0001 – 150	14
	2000-2001	Sweep net	0.03 – 77	12
		tube	0.02 – 301	36
South	1999-2000	sweep net	0.001 – 16	4
		Tube	0.1 – 6	2
	2000-2001	sweep net	0.002 – 36	15
		tube	0.002 – 6.5	3

P/Z ratios in tropical saline lakes are usually high. Burgis (1974), for example, estimated phytoplankton biomass to be 100 times zooplankton biomass on L. George. Mengestou & Fernando (1991) separated the zooplankton of L. Awasa into herbivorous and carnivorous components and estimated that phytoplankton exceeded zooplankton biomass by 25 to 146 times, suggesting large portions of the phytoplankton biomass were

uneaten by herbivorous zooplankton. Mean ratios on Sua pan, however, were generally, lower (Table 5.12) and were close to a mean value of 1.64 for 37 lakes representative of a wide variety of lake types (Sprules *et al.*, 1983). Large ranges in seasonal ratios, particularly in the middle basin, coincided with large increases in the biomass of the filamentous blue-green algae *Nodularia*, which comprised the majority of the phytoplankton biomass at the end of the flood periods (Chapter 4). While the low mean ratios might suggest a greater proportional utilisation of phytoplankton biomass by crustaceans, the crustacean biomass in this study includes benthic species and many of the dominant crustacean species, *M. belli*, the phyllopods and ostracods which are omnivorous. P/Z ratios may, therefore, be overestimates of phytoplankton utilization by the crustacean community.

5.4.3.3 Crustacean production

From life history data, growth curves for *B. spinosa* and *B. ornata* appeared exponential, as there was no inflexion in the growth curve and consequent decrease in the growth rate as maximum population size was approached (Fig 5.14). This is contrary to the sigmoidal growth patterns found by Mason (1963) for *Artemia salina* and Daborn (1975) for *Branchinecta gigas*. Hildrew (1985) also found a considerably decrease in the growth rate among individuals of *S. vitreus* in a long-term (32 days) cohort. Similar exponential growth patterns were, however, found by Marchant & Wiliams (1977) for *P. zeitziana*. Rapid growth of anostracans is part of a life history trait found in many inhabitants of temporary habitats (McLachlan, 1983; Hildrew, 1985). One of the most important aspects of a temporary habitat is the prediction of flood periods favourable for reproduction. In response to this, growth of the anostracans on Sua pan was very rapid and reproduction began relatively early (2 weeks after hatching) and at a modest size of approximately half a fully-grown adult. Average daily growth rates for both species of anostraca were estimated to be >50% dry weight d^{-1}, during the beginning of the flood periods in the north and middle basins. These are among the fastest growth rates recorded for temporary water invertebrates (e.g. Hildrew 1985, Daborn, 1975). P:B ratios, that ranged from 0.3 to 3.33, were similar to ratios from other studies (e.g. Marchant & Williams, 1977; Hildrew,

1985). Average daily production by *B. spinosa*, which was highest in the middle basin (7.5 (sw) and 9.6 mg m^{-2} d^{-1} (tb), during the 1999-2000 season and 102 (sw) and 94 mg m^{-2} d^{-1} (tb), during the 2000-2001 wet season), are among the highest estimates recorded for anostracan production. They exceed estimates of other similar species, such as *P. zeitziana* (30.9 mg m^{-2} d^{-1}) and *S. vitreus* (5.7 mg m^{-2} d^{-1}) (Marchant & Williams, 1977; Hildrew, 1985) and are amongst the highest production rates estimated for any crustacean species in African tropical lakes (e.g. Burgis, 1974; Gras & Saint-Jean 1983; Vareschi & Jacobs, 1984; Irvine & Waya, 1999). Average daily rates for *B. ornata* on the middle pan were considerably lower, estimated at 3.4 (sw) and 4.1 mg m^{-2} d^{-1} (tb) during the 1999-2000 wet season and very similar to average daily production estimates for the species in the north basin at the beginning of the 1999-2000 wet season. High mortality as a result of predation by Greater flamingo may account for much of anostracan production (Chapter 6).

Seasonal crustacean production on Sua pan was highest in the north basin owing, mainly, to the fact that it was the longer lasting lake but also because of the very high production totals contributed by *M. belli* and *L. Africana* (Table 5.11). Average daily production for *M. belli* was highest during the 2000-2001 wet season, at 207 (sw) and 265 mg m^{-2} d^{-1} during the nine month period from October 2000 to June 2001. Three orders of magnitude separate these estimates and those of *M. micrura* in L. Chad (2.5m deep), which were about 3.5 mg m^{-2} d^{-1} during the years 1964, 65 (Leveque & Saint-Jean, 1983), and approximately 50 times higher than daily production of *Thermocyclops hyalinus* in L. George (Burgis, 1974). *M. belli* production rates were even higher in the middle pan during the 1999-2000 wet season and contributed to the highest total production rates (an average of 620 mg m^{-2} d^{-1}) for the eight month season. Production for *L. africana* in the north basin was also amongst the highest recorded. Average daily production there for the whole flood period (Dec 1999 to June 2001) was estimated at 54 (sw) and 75 mg m^{-2} d^{-1} (tb) compared with a maximum rate for the same species, with the same average daily P:B ratio, on the 2-3 times deeper Lake Nakuru of 219 mg m^{-2} d^{-1} (Vareschi & Jacobs, 1984). There is no doubt that production would have increased at the beginning of the season in the north basin owing to the contribution by conchostracans.

Assuming that its production rate was similar to that of the anostracans, total production may have been approximately 0.5 g m^{-2} for the 1999-2000 wet season.

The P:B ratio for ostracods (0.33), calculated from the P:B-adult dry weight relationship (Fig. 5.2) may have been an over-estimate considering the ratio calculated from the regression equation of a similar relationship, calculated for small invertebrates by Banse & Mosher (1980), was 0.06. Although ostracod production was, therefore, overestimated according to Banse & Moshers relationship, the regression was based on data from temperate invertebrates and tropical organisms are likely to have higher P:B ratios as a consequence of higher temperatures (reviewed in Talling & Lemoalle, 1998). In contrast, production for *D. barbata* may have been underestimated owing to a relatively low average P:B ratio, calculated for the species by Hart (1987) in a lake at a much higher latitude and therefore lowers seasonal temperatures.

Total crustacean production rates estimated in the Makgadikgadi are similar or greater than some of the most productive saline lakes in tropical and sub-tropical Africa (Burgis, 1974; Gras & Saint-Jean 1983; Vareschi & Jacobs, 1984; Mengestou & Fernando, 1991) and maximum totals (Table 5.11) compare with estimates of annual zooplankton totals in some of the Great lakes of East Africa that have a production zone two to three orders of magnitude deeper (e.g. Irvine & Waya, 1999). There is no doubt, therefore, that during long seasonal flooding, Sua pan contains sufficient crustacean biomass that is turned over at a rapid rate to provide avian planktivores with one of the most abundant food sources found anywhere in Africa. This food source is an essential part of a rare and highly sensitive breeding regime of a Greater flamingos population that migrate to Sua pan on such occasions (Chapter 6).

Chapter 6

The breeding success and feeding ecology of the Makgadikgadi Flamingo populations

6.1 Introduction

6.1.1 Flamingo food and feeding

6.1.1.1 Greater Flamingo

The Greater Flamingo is a secondary consumer with a diet comprising of a wide variety of small benthic invertebrates and zooplankton, mainly crustaceans (Jenkin, 1957; Taylor, 1980; Johnson, 1983; Vareschi & Vareschi, 1984; Britton *et al.,* 1986). Filter feeding mechanics and kinematics have been studied in detail by numerous authors (Jenkin, 1957; Bildstein *et al.*, 1993; Zweers *et al.*, 1995). A large proportion of feeding occurs at night and feeding behaviour varies between occasional surface 'skimming' in deep waters to 'sweeping' their bills back and forth along the benthic surface of shallow waters, using their feet to disturb and suspend sediment and benthic invertebrates when 'stamp feeding' (Britton *et al.,* 1986; Bildstein *et al.,* 1993). Flock size and time spent feeding are influenced by invertebrate type, abundance and their spatial and temporal patterns of distribution (Britton *et al.*, 1986; Arengo & Baldassarre, 1995; 1999). At high densities, Greater Flamingo have a considerable impact on food availability as well as the physical and biological interactions that control benthic invertebrate abundance (Arengo & Baldassare, 1995; Comin & Hernandez, 1997; Glassom & Branch, 1997*a*; *b*). Glassom & Branch (1997*a*) estimated that, by excluding Greater Flamingo from areas in two Namibian coastal lagoons, macro-invertebrate densities increased by three times the densities of sub-tidal areas where Greater Flamingo were feeding. The daily food requirements (of mainly copepods) for Greater Flamingo, on Lake Nakuru, was estimated to be 82 g dry weight $bird^{-1}$ (Vareschi & Vareschi, 1984). This feeding rate was calculated from an equation based on the relationship between the amount of food required to sustain existence metabolism or the basal metabolic rate (BMR) and body mass, (Kendeigh, 1970). BMR energy requirements were converted to a higher energy cost of free existence by a factor of 1.5 and by 1.25 to allow for 80% food assimilation efficiency.

6.1.1.2 Lesser Flamingo

Lesser Flamingos are primary consumers relying almost entirely on blue-green algae (Cyanophyta) and diatoms. They do so, with great efficiency, using their highly specialized bills that contain finer lamellae and deeper keel than that of a Greater flamingo bill (Jenkin, 1957;Vareschi, 1978). Feeding may alternate between filtering the surface layers in deep waters to skimming the benthic surface in shallower waters (Ridley *et al.*, 1955; Tuite, 1978; Vareschi, 1978). Feeding efficiency and energetics have been analysed using captive birds and by indirect estimates (Pennycuick & Bartholmew, 1973; Vareschi, 1978). Pennycuick & Bartholmew (1973) estimated the metabolism of feeding Lesser Flamingos to be approximately 1400 kJ day^{-1} (391 kcal d^{-1} or 89.8 g DW algae and diatoms d^{-1}), from an equation based on the relationship between BMR and body mass in Lasiewski & Dawson (1967). They presented energy surplus as a linear function of two variables, the proportion of the day spent feeding and the food concentration in the water. After determining the energy content of their food and calculating filtration volume, efficiency and pumping rates, and assuming a food assimilation efficiency of 80%, it was calculated that if Lesser flamingos spent at least 80% of their time feeding, a minimum algal density of 125 g dry weight m^{-3} was required to maintain adult birds in normal activity. These estimates were, however, based on many assumptions and made no allowance for the efficiency of the filtering system and the assimilation efficiency of different food types (e.g. filamentous cyanophytes and diatoms). Vareschi (1978) made direct measurements of daily algal intake from captive birds feeding in tanks of known concentrations and calculated that Lesser Flamingo feeding efficiency (the proportion of food filtered from water) was 64-86% when *Spirulina* was dominant on Lake Nakuru. From phytoplankton removal rates and by applying them to populations of known size and algal concentrations in Lake Nakuru, Vareschi (1978) also determined an algal density of >100 g dry weight m^{-3} was necessary to maintain a population on Lake Nakuru. He estimated that adult Lesser Flamingos, feeding for 12.5 hours a day, consumed 72 g DW (1312.5 kJ or 314 kcal) d^{-1} at algal concentrations of between 150 and 200 mg l^{-1}. This estimate was similar to a daily energy requirement of 67 g DW d^{-1} he calculated for an adult Lesser flamingo, based on the relationship between body mass and basal metabolic rate (Kendeigh, 1970), converted to the energy costs of free existence by

a factor of 1.5 and allowing for an 80% food conversion. With an average population density of 0.023 birds m^{-2} (915000 birds) on L. Nakuru at the time (average depth of 2.3 m), this was equivalent to a mean areal consumption of 1.6 g DW m^{-2} d^{-1}.

6.1.1.3 Variability in food abundance and flamingo distribution

A complex interrelationship between water levels, salinity and productivity controls food abundance for both species of flamingo (Pennycuick & Bartholomew, 1973; Tuite, 1978; Vareschi, 1978; Arengo & Baldassare, 1998,1999; Cezilly *et al.*, 1995). Food density is the primary controlling factor for flamingo density. Rapid variations in food availability and depletion of resources within and between sites over short and long term periods is thought to be linked to the highly nomadic nature of both flamingo populations in Africa (Brown, 1959; Brown *et al.*, 1982; Vareschi, 1978; Tuite, 1979, 2000). Based on theoretical calculations of minimum food concentrations required by non-breeding birds (80 g to 150 g DW m^{-3}) and on a good correlation between flamingo spatial distributions and algal densities, Pennycuick & Bartholomew (1973) suggest that flamingo movements are triggered by algal concentrations. Vareschi (1978) also found good correlations between flamingo numbers and algal densities, although numerous movements between East African saline lakes are not related to algae densities.

While both species are associated with numerous inland saline lakes and coastal lagoons in southern Africa (e.g. Simmons, 1996, 2000; Hancock, 1990; Borello *et al.*, 1998; Simmons *et al.*, 1998; Anderson, 2000*c*), very little is known about flamingo food and feeding ecology in the sub-continent.

6.1.2 Flamingo breeding

6.1.2.1 Breeding productivity and controlling factors

Breeding numbers and colony productivity (fledglings per breeding pair) depend, predominantly, on seasonal flooding and water levels, which in turn control salinity, food availability and freedom from mammalian predation (Brown, 1959; Brown *et al.*, 1973; Berry, 1972; Cezilly *et al.*, 1995, Simmons, 1996). Because they lay only one egg, flamingos cannot offset poor breeding conditions by reducing clutch size in order to increase offspring quality. Breeding adults are, therefore, unable to 'buffer' fluctuations in water level and food scarcity and when energy costs are high and food availability is low, the survival and future reproductive potential of these long-lived birds is jeopardised (Cezilly, 1993; Cezilly *et al.*, 1996; Tavecchia *et al.*, 2001). Rapid evaporation of water from temporary salt pans, reduces food availability and can force adults to abandon eggs and chicks, often resulting in high or complete mortality of young birds (Berry, 1972; Brown, 1975; Archibold & Nott, 1987; Broekhuysen, 1975). Lesser Flamingo breeding is particularly vulnerable because their nests are built on the mud surface of the pans and are, therefore, susceptible to flooding (Brown, 1973; Berry 1972; Hancock, 1990). Pennycuick & Bartholomew (1973) argued that the most important factor controlling breeding attempts is local food density. They estimated a minimal algal density of 250 g DW m^{-3} (twice the normal concentration requirement of free existence) was required in order to satisfy higher energy costs during breeding, spending only 40% of their daily budget feeding. Metabolic rate among birds during the breeding season, particularly among birds feeding large chicks, was calculated by King (1974) and Drent & Daan (1980) to be an average of four times, and as much as nine times, the BMR. Decreased energy assimilation during Greater Flamingo laying and incubation periods has been observed to affect nest attendance, especially among females and, in some cases, lead to nest desertion and breeding failure (Cezilly, 1993). Food abundance also has important implications for chick survival and long-term recruitment to the breeding population. By comparing Greater Flamingos breeding success over a number of years, Cezilly *et al.* (1995) found that high water levels correlated with heavier chicks owing to increased food availability. More importantly, a higher recruitment rate was observed from cohorts

that were heavier at fledging. Body condition when fledging was also shown to have an important influence on post fledging dispersal and survival (Pradel *et al.*, 1997; Barbaud *et al.*, 2003).

6.1.2.2 Breeding in southern Africa

Breeding in East Africa occurs, predominantly, on lakes Natron and Elmenteita for Greater Flamingo (Brown 1959; 1973; Brown *et al.*, 1973) and on the saline mud flats of Lake Natron for Lesser Flamingo (Brown, 1959; 1973; Brown & Root, 1971). The main breeding sites in southern Africa are the seasonally flooded Etosha saltpan in Namibia and the Makgadikgadi saltpans in Botswana (Berry, 1972; Hancock, 1990; Simmons, 1996). Breeding attempts on Etosha pan occur, approximately, every three years, while successful breeding occurred only five times in forty years (Simmons, 1996). Juveniles that frequently appear at feeding sites around southern Africa, when no breeding has been recorded elsewhere in the sub-continent, are considered to have originated from the Makgadikgadi (e.g. Tarboton, 1993; Simmons, 1996; Anderson, 2000*c*). Indeed, breeding attempts on Sua pan, Makgadikgadi occur more frequently than on any other breeding site in southern Africa (Simmons, 1996, 1997, Tim Liversedge, pers. comm.).

6.1.2.3 Abundance and breeding success on Makgadikgadi

The establishment of ephemeral standing waters on the Makgadikgadi triggers the mass migration of both Greater and Lesser Flamingo that arrive in their hundreds of thousands (Hancock, 1990; Simmons, 1996; 2000; Borello *et al.*, 1998). Large flocks have been recorded on numerous occasions since the 50s (e.g. Smithers & Paterson, 1959; Smithers, 1964), while early observations of the presence of young on Sua pan and evidence of ancient nesting sites suggests a long history of flamingo breeding on the Makgadikgadi (Parker, 1975; Ginn, 1976; Hancock, 1990). The first published record of breeding was, however, not until 1978, when an estimated 35000 Greater flamingo and 1500 Lesser flamingo bred in the southern part of Sua pan (Robertson & Johnson, 1979). This was the largest recorded breeding population of Greater flamingo in Africa at the time. Since then a number of breeding events, with similar or larger numbers, have been observed there (Hancock, 1990; Herramans, 1993; Tim Liversedge, unpublished reports to the Dept. of

Wildlife, Botswana). After exceptional rains, extensive flooding facilitates continuous breeding so that laying and hatching is staggered and very large colonies of breeding pairs form (Herremans, 1993; Tim Liversedge, pers. comm.).

6.1.3 Migration of Makgadikgadis' flamingos

The geographical origin of the flamingos that migrate to the pans is largely unknown (Hancock, 1990; Borello *et al.,* 1998). It has been suggested that the birds migrate from a number of sites around southern Africa (Williams, 1993; Simmons, 1996, 2000; Borello *et al.,* 1998; Anderson, 2000*c*). Populations of Greater and Lesser flamingo in southern Africa, estimated at 55000 Greater and 40000 Lesser flamingo (Dodman & Taylor, 1995, Simmons 1997) do not, however, account for the large numbers recorded on Sua pan in years of exceptional rainfall (Simmons, 1996; Borello *et al.*, 1998). Brown (1973; 1975) argued against the theory of flamingo migration between East and southern Africa owing to the fact that migration over land only occurs at night and that the distance is too great for one non-stop flight considering there are insufficient stopover sites en route. Large population increases on Sua pan (e.g. Parker, 1975) in the past have, however, corresponded with population declines in East Africa (Tuite, 1981), and strongly suggest such interchange (Borello, *et al.,* 1998; Simmons, 2000). Apart from the well-known non-breeding habitats for the southern African populations (Walvis Bay, Namibia and Kamfers Dam in South Africa for example) collectively, small endorheic wetlands also provide an important habitat network for flamingos in the sub-continent (Allan *et al.*, 1995; Anderson, 2000*c*; Breen, 1991). The conservation of flamingos on small ephemeral pans and some perennial wetlands around southern Africa is of concern owing to the lack of formal, effective protection of the majority of these sites (Breen, 1991; Anderson, 2000*c*) that are under increasing threat (Davies & Day, 1986; Allan, 1987; Breen, 1991; Allan *et al,* 1995).

6.1.4 Aims and objectives

This chapter concerns some of the feeding and breeding habits of Greater and Lesser Flamingos on Sua pan and attempts to link algal and crustacean biomass and productivity with, respectively, Lesser and Greater food availability and breeding success during two successive breeding seasons. The objectives were to:

1. carry out monthly aerial photographic censusing of Greater and Lesser flamingo populations and estimate total population, breeding numbers and breeding productivity during two successive breeding seasons;
2. identify the diet of both Greater and Lesser flamingo on Sua pan from opportunistic crop samples and faecal samples;
3. measure food consumption on Sua pan by both Greater and Lesser flamingo using feeding rates and individual energy requirements from the literature
4. establish a theoretical model of the relationship between population numbers and breeding success of each species on Sua pan and their respective food densities; and
5. study the behaviour and patterns of flamingo movements from the Makgadikgadi and their dispersal throughout southern Africa by satellite tracking individuals of each species.

6.2 Materials and methods

6.2.1 Population surveys

The relatively large size, bright colour and habit of concentrating into large flocks has enabled surveys of flamingos to be done from the air over the soda lakes of East Africa (Grzimek & Grzimek, 1960; Bartholomew & Pennycuick, 1973; Tuite, 1978; Vareschi, 1978; Woodworth *et al.*, 1997). During these studies standard photographic and data analyses techniques were adopted. Flock aggregations and positioning on Makgadikgadi were, however, somewhat different to those on the soda lakes of East Africa. With the exception of some concentrations along the shores of the deep north basin, the majority of flamingos on Sua pan were widely distributed in flocks of variable size owing to the very shallow nature of flooding. Photographic protocols were, therefore, modified slightly in this study, although the basic principles were similar.

Photographic censusing of Sua pan and adjacent pans was carried out over the coarse of the three year study period (Table 6.1). The first census of the breeding colonies was done during the 1998-1999 wet season, from a Cessna 210 light aircraft. During the 1999-2000 wet season six aerial surveys were carried out at roughly 1-2 month intervals, censusing total population on four occasions and numbers of breeding adults and chicks on five occasions. Owing to the extent of flooding during the 1999-2000 wet season and for cost and logistical reasons, some of the smaller pans adjacent to Sua pan (that may have held a few thousand birds) were omitted in February and March 2000. Two full censuses were also carried out during the 2000-2001 wet season. A Cessna 206 was chartered to conduct five of the six surveys made during the 1999-2000 wet season owing to the extent of the floods and the time needed to survey the entire Makgadikgadi complex. Two surveys (in May 2000 and April 2001) were carried out using a microlight, when it was feasible to cover the total area at a much slower fight speed.

Table 6.1 Dates and type of Censuses made between January 1999 and March 2001.

Year	Date	Census Type
1999	Jan 2nd	Breeding
	Dec 20th	Population
	Dec 27th	Breeding
2000	Feb 4th	Population & Breeding
	March 18th	Population & Breeding
	April 25th	Population & Breeding
	May 30th	Breeding colony
2001	Feb 12th	Population & Breeding
	April 31st	Breeding

From previous aerial surveys of the area it was apparent that, generally, both species aggregate in large flocks that were patchily distributed at various distances from the shoreline owing to the very shallow nature of the lakes on Sua pan. One of the major problems that influenced what photographic protocol to use when carrying out the surveys over Sua pan was the extreme sensitivity of flamingos to planes. Even at 2000 ft the flamingo flocks would take flight and remain in flight until the plane was out of range for photography. After numerous trial runs it was decided that the traditional transect method recommended for population censuses of this kind, using a fixed camera (e.g. Norton Griffiths, 1978; Bonifica, 1992), may be prone to large inconsistencies owing to the moving flocks. Instead, a combination of the transect method (when birds were highly dispersed and at low density) and the 'total count' method (Woodworth *et al.*, 1997), whereby each discrete flock found was photographed in full, comprised the survey protocol during each census.

Despite the disturbance factor, flight altitude above lake level was kept at 1000 ft while photographing the population, in order to distinguish between the two species. Altitude was increased to >1500 ft above lake level when photographing the breeding colonies and direct flights over the colonies were avoided in order to reduce disturbance. Professional 35 mm Kodak slide film was used in a Canon 1000N automatic camera with a 55-70 mm Canon lens. A number of different photographic methods were used, depending on the size and density of flamingo aggregations:

1. When flocks were small (<1000) they were scored by direct counts;

2. When large dense flocks were encountered the entire flock was photographed with a series of overlapping photographs where necessary. The number of each photograph corresponded to notes and GPS co-ordinates, taken during the flight; and

3. On the rare occasions when densities were low and flamingos were widely dispersed over a large area, a 'sample vertical photography' method, similar to that used by Bartholomew & Pennycuick (1973) and Tuite (1978), was adopted. Areas occupied by flamingos were measured by flying line transects across the length and width of the areas covered and estimating the distance of both using flight time and airspeed. During each transect a series of non-overlapping photographs were taken every 20 seconds. Each photograph was a sample unit and the area covered by each photograph was an estimated 47000 m^2.

From the processed slides, flamingos were counted from projected images on grid wallpaper, using a Leica projector. The dots (flamingos) were counted and ticked with a marker pen to avoid recounting. Slides from different photographic techniques were counted in slightly different ways:

1. Small flocks were counted in their entirety from projected images (e.g. Fig. 6.1*a*);

2. When flocks were very dense and contained tens of thousands of birds (e.g. Fig. 6.1*b*), sample squares were chosen at random from the total area covered by the flock and each sample unit was counted. The number of squares covered by each flock was multiplied by an average number per square unit and the standard deviation (SD) was calculated from the variance around the mean. Areas of duplication among overlapping photographs of the same flocks was accounted for. At least 50% of the area covered by each flock was sampled in such cases. Numbers breeding on the colonies were also counted in this way; and

3. For the low-density populations (Fig. 6.1*c*), a total 40 to 50 photographs were chosen randomly from the total number taken during both transects and sample area counted was at least 10% of the total area (Table 6.2). Flamingo numbers on each slide were counted as above and a mean number per sample unit was calculated. Together with a total estimate of the low-density area, an estimate of the total flamingo population in the area was calculated. Standard deviations were calculated for each population from the variance around the mean sample number, which was calculated by the equation;

$$s^2 Y = N(N - n)/n \,.\, s^2 y$$

where $s^2 Y$ is the variance of the total flock number, N is the total number of sample units, n the number of sample units counted, Y the population estimate, y the number of birds counted in a sample unit, and $s^2 y$ the variance of y (Jolly, 1969).

Estimates of biomass for Greater and Lesser Flamingo were taken from the average weight of individuals measured during a capture and ringing exercise in July 2001 and from opportunistic weighing of individuals that collided into veterinary cordon fences and power lines. Average mass of each species was converted to biomass density per m^{-2} based on the number of each species present and lake size (Bartholomew & Pennycuick 1973, Tuite 1978). Lake size estimates are provided in Chapter 2.

Table 6.2 Survey and counting parameters for areal photographic censusing of low-density flamingo populations. Area covered is given in km^2 and total area of the wetland on Sua pan, on occasions when it could be calculated, are also given in parenthesis.

Date	Species	Survey area in km^2 (Wetland area in km^2)	Sample area (km^2)	Sample fraction
4th Feb, 2000	Lesser	9.4	2.01	21.4 %
7th March, 2000	Lesser	16.7	1.92	11.5 %
7th March, 2000	Lesser	23.9	2.42	10.2 %
18th March, 2000	Lesser	20.2	2.66	13 %
25th April, 2000	Lesser	11.5 (3317)	1.84	16 %
4th Feb, 2001	Lesser	26.2 (304)	2.49	9.5 %

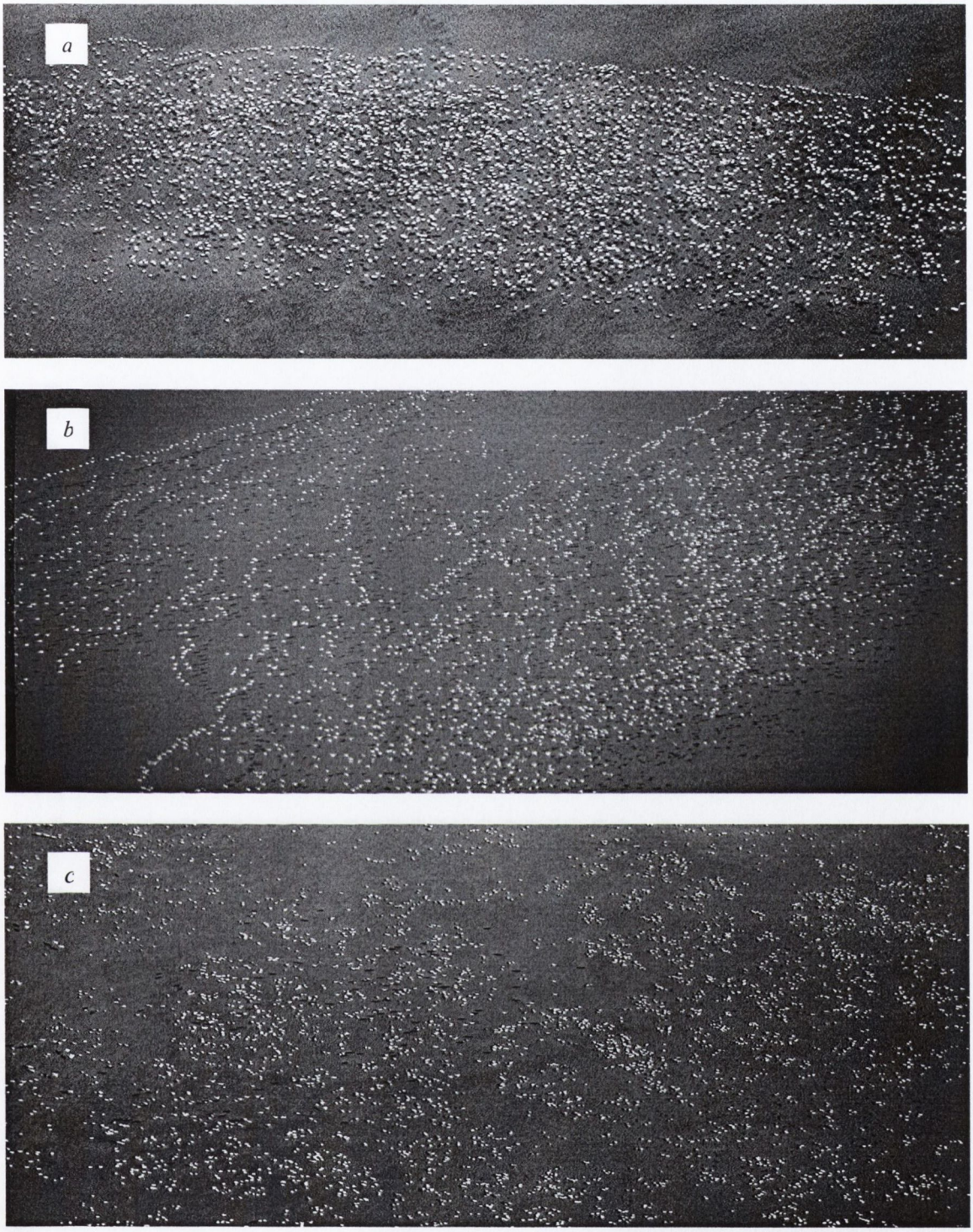

Figure 6.1 Aerial photographs of flamingo flocks of different size and density; image ***a*** is one of four overlapping photographs covering a very large flock, ***b*** is a photograph containing an entire flock of smaller size and ***c*** is a typical photograph from a series of 'vertical sampling' photographs covering widely dispersed, low density distributions.

Fig. 6.1

6.2.2 Breeding population and breeding success

Breeding colonies were photographed and numbers of breeding pairs were monitored during most aerial surveys (Table 6.1). Series of overlapping photographs were taken of the entire colonies and the slide images projected onto grid wallpaper for counting (e.g. Fig. 6.2). In addition, close up 'shots' were taken of parts of the colonies, with a 70-300 mm zoom lens, in order to distinguish between the number of nests and the number of birds on and around the nests. Close up photographs were also taken of the crèches when the chicks emerged and, again, numbers were counted from projected slide images on wallpaper. Breeding success was estimated as the ratio of fledging chicks to total number of breeding pairs on the colony. Egg success was the ratio of the number of young in the crèches to the number of eggs laid. The number of dead chicks and abandoned eggs on the colonies were counted shortly after the breeding season. With no close ground observations during the breeding season, it was impossible to accurately count the number of eggs laid, numbers of double clutches and egg and chick mortalities and estimates from the aireal photographs assume some degree of error.

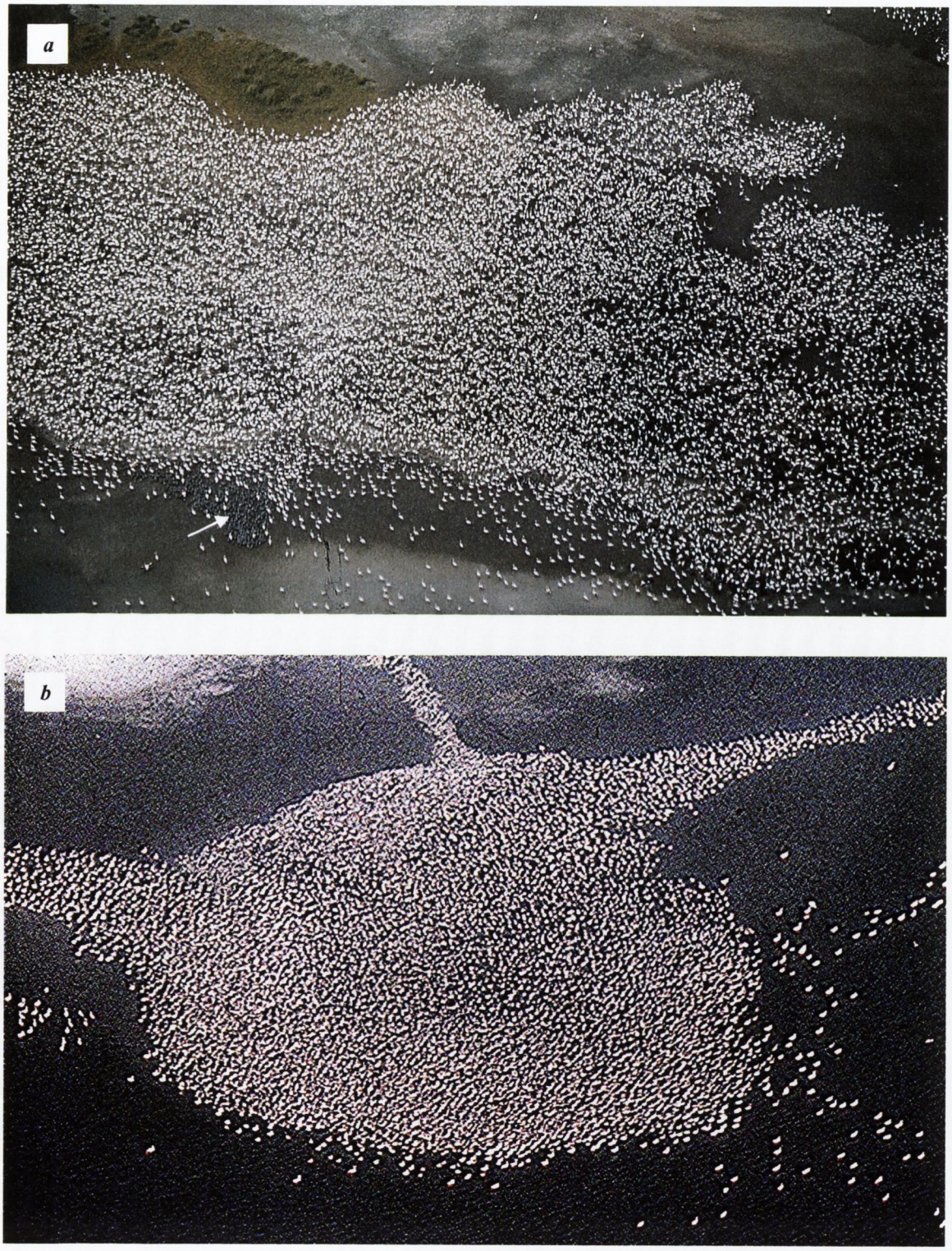

Figure 6.2 Photograph of part of a Greater flamingo colony (*a*) and a nearby crèche (*b*) used to count the number of breeding adults and chicks. The white arrow indicates small grey chicks forming a crèche.

From measurements made in both East Africa (Brown & Root, 1971) and Namibia (Berry, 1972), Lesser Flamingo eggs average 80 x 50 mm in size and weigh approximately 100 g. Greater Flamingo eggs, measured on colonies in East Africa, averaged 88 x 56 mm (Brown & Root, 1971) corresponding to a weight of approximately 135 g. Average dry weights (DW) for Lesser and Greater Flamingo eggs were, therefore, calculated as, respectively, 30.3 g and 40.9 g (0.303W = DW; calculated from average bird data, Cummins & Wuycheck, 1971). Egg numbers were approximated from the total number of pairs breeding during each season. Seasonal egg production was calculated by the equation,

$$DW_{egg} \cdot N_{egg}$$

Average body mass for Greater Flamingo fledglings was assumed similar to those raised on the Camargue, in southern France, that averaged 2.32 Kg WW (n = 1575) for five breeding seasons (Barbraud *et al.*, 2003). Assuming average weight for Greater Flamingo adults was approximately 3 kg (Brown *et al.*, 1982) and fledglings weigh approximately 77% of adult weight. Accordingly, Lesser Flamingo fledglings were calculated to be 1.34 kg (77% of the average adult weight on Sua pan of 1.74 kg). Equivalent dry weights were calculated as 702 g and 527 g for, respectively, Greater and Lesser Flamingo fledglings (WW – DW conversion of 0.303, Cummins & Wuycheck, 1971). Assuming chicks hatch at approximately the same weight as egg weight and fledge at least 70 days later (Brown & Root, 1971; Brown, 1959), chick production was calculated for each species by:

$$P = (N \cdot DW) / d$$

where P is production (mg DW m^{-2} d^{-1}), N is total number of chicks for each species, DW is weight of juveniles at fledging and d is the number of days required for chicks to fledge.

Flamingo breeding productivity (g m^{-2} yr^{-1}) was estimated by the summation of both egg and chick production.

6.2.3 Flamingo diet

6.2.3.1 Crop samples

Opportunistic crop samples were taken from flamingos that were killed on overhead power lines and radio mast guide wires on and close to Botswana Ash (Pty.) Ltd. soda Ash mine, and along veterinary cordon fences that cross the middle basin, bisecting one of the main nocturnal flight paths of breeding flamingos. Crop contents were weighed, preserved and later examined under both dissecting and compound microscopes to determine food type. Greater Flamingo crop contents were placed in a sample bottle with 200 ml of water, the contents mixed thoroughly and ten 5 ml samples removed and placed under a dissecting microscope for species counts. Species abundance was converted to biomass by length-weight relationship equations (Chapter 5) and the proportion of total biomass calculated for each species. Similarly, five samples from diluted Lesser Flamingo crop samples were placed on a haemocytometer and the different species counted. Abundance was then converted into proportional biomass for each species and the proportional abundance of total biomass calculated. A total of six Greater and 13 Lesser flamingo crops were examined between December 1999 and June 2001.

6.2.3.2 Faecal samples

In clear shallow water conditions it was possible to identify and distinguish between Greater and Lesser faeces on the sediment floor. When faeces were found during weekly sampling trips, they were carefully removed from the lake floor, washed to remove any benthic algae or crustacean contamination and preserved for examination under dissecting and compound microscopes. Species were identified as much as possible and proportional abundance of each species was estimated. A total of 24 Greater flamingo samples and 37 Lesser flamingo faecal samples were taken and analysed between December 1999 and June 2001.

6.2.4 Flamingo energy requirements

Theoretical estimates of food requirements for each species were established from consumption figures in the literature. Minimal daily food consumption (kg dry weight d^{-1}) by the Greater and Lesser Flamingo populations on Sua pan were estimated by multiplying the feeding rates required for free existence of, respectively, 82 g DW (1494.4 kJ) and 72 g DW (1312.5 kJ) d^{-1} (Vareschi, 1978; Vareschi & Vareschi, 1984) by population numbers. This assumes the algae on Sua has the same calorific equivalent of *Spirulina*, 4360 cal g^{-1} DW (Vareschi, 1978). Food consumption rates used in the 2000-2001 wet season were 10% less, 75 g DW (1367 kJ) and 66 g DW (1204 kJ) d^{-1} for, respectively, Greater and Lesser Flamingo, to allow for young flamingo that weighed less and had lower filtering rates than adults (Vareschi 1978). Values for food consumption in the lake were then converted to volumetric (mg m^{-3} d^{-1}) and areal consumption (mg m^{-2} d^{-1}) for, respectively, flood volume and area on Sua pan and its surrounding pans. Approximate volumes of Sua pan, for both seasons, were calculated from estimates of flooding areas and a mean depth of 0.5 m during the 1999-2000 wet season and 0.3 m during the 2000-2001 wet season (Chapter 2).

Food consumption to meet energy requirements during breeding were calculated by multiplying the BMR of both species by four, the average increased rate of metabolism among breeding birds (King, 1974; Drent & Daan, 1980). BMR was calculated by:

$$EM = \text{O.5404 x } W^{0.7545},$$

where EM is BMR in kcal d^{-1} and W is weight in g (Kendeigh, 1970). BMR for Greater Flamingo was 43.7 g DW d^{-1} and for Lesser Flamingo is 35.5 g DW d^{-1}. Multiplied by a factor of four gives a consumption rate during breeding of 175 g DW d^{-1} and 142 g DW d^{-1} for, respectively, Greater and Lesser Flamingo.

6.2.5 Satellite tracking flamingo from Sua pan

In July 2001, we began the first satellite-tracking project of flamingos in southern Africa in an attempt to monitor their movements from the Makgadikgadi after an exceptional breeding season. A total of 28 flamingos were caught on Sua pan using a noosing method, similar to the method used in East Africa (Brooks Childress, personal communication) and South America (Bill Conway, personal communication). Using 80 g and 30 g PTT satellite telemetry devices, we tagged, respectively, five Lesser and three Greater Flamingos. The devices were attached to the birds using a figure-of-eight style harnessing technique with Teflon ribbon, described by Nagendran *et al.* (1994). The transmission cycles of each device were set at 8 hours on – 158 hours off, for 6 months, switching to a cycle of 8 hours on – 44 hours off, for the time estimated to coincide with the six month period around breeding and migration. The PTT cycles were offset from the 24-hour orbit cycles of the receiving satellites, to avoid possible transmission at a 'time-window' each day with few or no overpasses. 'On' periods, therefore, occurred at different times of the day, alternating between nocturnal and diurnal transmissions. All data collected was transmitted through the Argos satellite system. According to the ARGOS system, location accuracy varies according to the PTT signal strength and the number of receiving satellites (maximum of five) during each transmission. The most accurate locations come from LC 3 quality transmissions, 67% of which are within 150 m of the 'real' positions (of known ground positions). 67% of LC 2 quality transmissions are within 350 m and 67% of LC 1 transmissions are within 1000 m. Location quality decreases further in order of LC A, and LC B quality data. Prior to their deployment, each PTT device was tested for accuracy by activating them and comparing the processed location data with that of their know location (GPS co-ordinates on the ground). 23 from a total of 43 PTT locations were within 1 km of the real position. The mean distance of LC 3, LC 2, and LC 1 data was, respectively, 502, 525 and 905 m. LC A and LC B location data averaged 1052 and 5980 m, respectively.

6.3 Results

6.3.1 Population abundance

6.3.1.1 Greater Flamingo

Greater Flamingo population numbers increased from 3307 in December 1999 to a maximum estimate of 57875 in March 2000 (Table 6.3). In December 1999, flocks were confined to the north basin and some of the small pans to the south of Sua pan. For the rest of the season, apart from high concentrations at the breeding colonies, flocks were widely dispersed across the middle and, especially, the south basins, with small numbers situated on other pans to the south and west of Sua pan. Most of the counts in February, March and April were made from slides of adults on the breeding colonies in the south of the pan, while some individuals were counted from the air among larger Lesser Flamingo flocks. Greater Flamingo biomass density on Sua pan was based on an average weight per adult of 3.15 kg (based on the average of 3.4 ± 0.08 (95% CL) kg for males and 2.9 ± 0.16 kg for females, n = 13) and total flood area on Sua pan and the pans adjacent to Sua (Table 6.3). Although the population increased 20 fold from December 1999 to April 2000, biomass densities remained very similar, estimated at, respectively, 55 and 50 mg m^{-2}, owing to the large increase in flood area during that period. These densities were equivalent to dry weight biomass densities of 16.7 mg and 15 ± 0.4 mg DW m^{-2}, assuming that fresh weight is converted to dry weight by a factor of 0.303 (Cummins & Wuycheck, 1971). As the flood began to recede, biomass densities increased. Using an average population estimate (SD) for the period February to April 2000, of 53786 ± 2274 (from results in Table 6.3), densities increased to 37 ± 1.6 mg DW m^{-2} by August 2000. In late September only 365 km^2 of the north basin remained flooded. Densities may have increased to 200 ± 10.5 mg DW m^{-2} in September 2000, assuming a population of 76284 (average population estimate for 2000 of 53786 plus 22498 juvenile numbers) remained on Sua pan. A decrease in the population to an estimated 39332 was recorded in February 2001, the majority of which were concentrated in the north basin. Although many Greater

Flamingo had left by then, biomass density reached an estimated 124 ± 4 mg DW m^{-2} owing to their high concentrations on a rapidly disappearing lake.

Table 6.3 Population and biomass density ± Standard Deviation (SD) of Greater Flamingo on Sua pan and adjacent pans during the 1999-2000 and 2000-2001 wet season. The figures marked with * are average population estimates for the period February to April 2000 used to calculate biomass densities for June and August 2000.

	Survey Method				
Date	**Visual**	**Total counts**	**Total (adults)**	**Flood (km^2)**	**FW (mg m^{-2})**
1999-2000					
Dec 20th	540	2764	3307	190.5	55
Feb 4th	2850	48423 ± 2404	51273 ± 2404		
March 18th	1630	56245 ± 3021	57875 ± 3021		
April 25th	1234	50975 ± 1398	52209 ± 1398	3317.1	49.1 ± 1.3
June 24th			53786 ± 2274*	2142.4	79.1 ± 3.3
Aug 11th			53786 ± 2274*	1388.5	122 ± 5.16
2000-2001					
Feb 12th	3210	26122 ± 1,244	39332 ± 1244	304	407.6 ± 12.9

6.3.1.2 Lesser Flamingo

Lesser Flamingo numbers also increased dramatically during the 1999-2000 wet season, from 19753 individuals in December 1999 to an estimated maximum of 149397 in March 2000 (Table 6.4). Large flocks in the north basin comprised much of the December count, with small flocks scattered in the middle and some of the small pans around Sua pan. As flooding increased in 2000, a large proportion of the February counts comprised huge flocks that were distributed across the shallow waters of the middle basin, some of which required vertical photographic sampling (Fig. 6.1*c*). In these low density areas, flamingos were distributed at an average of 6194 ± 1818 (SD) individuals per km^{-2} (n = 5). An average weight per adult of 1.74 kg (based on the average of 1.9 ± 0.1 (SD) kg for males and 1.68 ± 0.15 kg for females in July 2001, n = 29) was used to calculate biomass densities for Lesser Flamingo (Table 6.4). Body weight did, however, vary seasonally. The average weight for six Lesser Flamingos killed on power lines upon arrival at Sua pan, in December 1999, was 2.3 ± 0.15 kg. Based on the average July weights dry weight biomass densities decreased from 54.5 ± 2.3 mg DW m^{-2} in December 1999 to 23 ± 2.2 mg DW m^{-2} in April 2000 with a large increase in flood area. Assuming the population remained similar to the average estimate for the period February to April 2000 (138855 ± 12862), densities increased to 53 ± 16 mg DW m^{-2} by August 2000 as the area of flooding decreased still further. Numbers increased to 157655 individuals in February 2001, with the vast majority concentrated in the north basin, resulting in a biomass density of 273 ± 32 mg DW m^{-2}.

Table 6.4 Population and biomass density ± Standard Deviation (SD) of Lesser Flamingo on Sua pan and adjacent pans during the 1999-2000 and 2000-2001 wet season. The figures marked with * are average population estimates for the period February to April 2000 used to calculate biomass densities for June and August 2000.

	Survey Method					
Date	**Visual**	**Total counts**	**Transect Est's**	**Total (adults)**	**Flood (km^2)**	**FW ($mg\ m^{-2}$)**
1999-2000						
Dec 20th	2,620	17133 ± 826	0	19753 ± 826	190.5	180.5 ± 7.6
Feb 4th	1,850	58423 ± 2404	65245 ± 6866	125518 ± 9270		
March 18th	600	62245 ± 3021	86552 ± 12,620	149397 ± 15641		
April 25th	2,300	70536 ± 1,725	68813 ± 11,951	141649 ± 13676	3317.1	74.3 ± 7.2
June 24th				138855 ± 12862*	2142.4	112.8 ± 10.5
Aug 11th				138855 ± 12862*	1388.5	174 ± 16.1
2000-2001						
Feb 12th	1210	34572 ± 856	121873 ± 17793	157655 ± 18,649	304	902.4 ± 106.8

6.3.2 Breeding success and flamingo productivity

6.3.2.1 Greater Flamingo

It was assumed that Greater Flamingo failed to breed during the 1998-1999 wet season because of their absence at traditional breeding colonies on the 2nd of January 1999. The pan dried up shortly after that, in early March, and a successful breeding attempt after the survey was deemed highly unlikely. During the 1999-2000 wet season, Greater Flamingo breeding occurred on a much larger scale (Table 6.5). On the 27th of December 1999, three small breeding colonies comprising an estimated 1130 Greater Flamingo nests with incubating adults, close to the Lesser Flamingo colonies in the south basin (Fig. 6.3). The colony was not counted again until an aerial survey on the 4th of February. By then these small colonies had grown in size to an estimated 2900 nests. In addition, a much larger colony, named 'Greater colony 1' (GC1), had formed on the western tip of a long sand island 12 km southeast of the Lesser Flamingo colonies (Fig. 6.3), on which an estimated 4347 nests were built (Fig. 6.4*a*). By the 18th of March, the small colonies close to the 'Lesser colonies' had disappeared and it appeared that the nests had been washed away by the higher water levels. It was assumed, however, that there had been enough time before the flooding in March to allow most, if not all, of the eggs to hatch and join nearby crèches. Numbers of flamingos on GC1 dramatically increased and an estimated 10932 nests had been added to the colony (Fig. 6.4*b*), which now numbered 15279 pairs of breeding adults. By then, an estimated 3845 chicks had hatched and surrounded the colony. With space for nesting sites decreasing, yet another colony, 'Greater colony 2' (GC2) was occupied by breeding adults on the northeast shore of the island (Fig. 6.3).

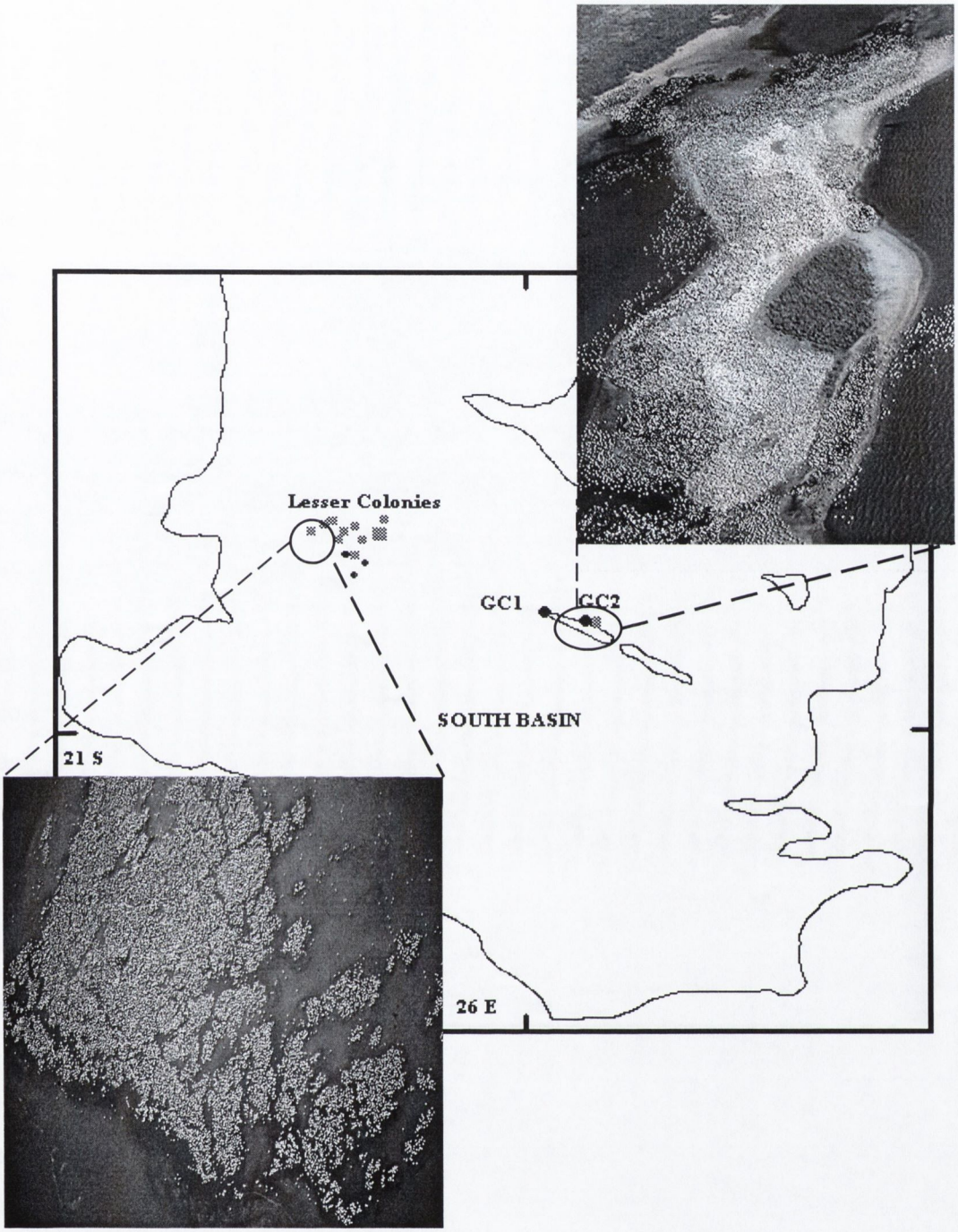

Figure 6.3 Map of the south basin illustrating the position of the Greater ● and Lesser ▒ Flamingo breeding colonies during the 1999-2000 and 2000-2001 wet seasons. The plates inset are examples of pictures taken of the colonies from the air.

A further 707 nests were counted on GC2 contributing to a total of 17986 breeding pairs at that time. On the 25th of April 5062 nests were occupied by adult Greater Flamingos on GC1 (Fig. 6.4*c*). These nests were part of the original colony, built before February 4th and were, therefore, occupied for a second time, adding to the total seasonal numbers breeding. 12411 chicks formed two large crèches either side of the colony. GC2 also increased in size and the numbers of breeding Greater Flamingo increased by a further 2927 pairs. Amazingly, GC2 also comprised thousands of Lesser Flamingos that were easily distinguished from the air by their smaller size and pink colouration and surrounded the larger white Greater Flamingo (Fig. 6.5*a,b*). The final aerial survey of the season, on the 30th of May, revealed that all nests were vacant on GC1 and a huge crèche had formed around the tip of the island with an estimated 13194 chicks (Fig. 6.3 *d*). Breeding also stopped on GC2 and two additional crèches were recorded around that colony numbering a total of 16133 chicks. It was, however, impossible to distinguish between the chicks of each species around GC2 and it was, therefore, assumed that the proportion of chicks in both crèches was similar to the respective breeding numbers of each species on the colony. Greater Flamingo pairs made up an estimated 18% of the colony and so the number of Greater Flamingo chicks in these crèches was calculated at 2904. During the 1999-2000 wet season, an estimated 83% of the maximum recorded population took part in breeding and chicks raised were an estimated 77% of eggs laid. Chicks raised were also estimated at 39% of the breeding population (or 32% of the maximum recorded population).

In comparison with the large breeding event of 2000, very few Greater Flamingo attempted to breed during the 2000-2001 wet season. A total of 651 occupied nests were recorded on the open mud surface just south of the Lesser Flamingo colonies, on February 12th 2001. It was assumed that few chicks survived to fledge owing to the rapid drying of the water later that year, although it was impossible to distinguish surviving chicks from those of Lesser Flamingo during the April survey. A very small proportion of the 2000-2001 wet season population took part in breeding (<0.02%) and breeding success may have been less than 20% of breeding pairs.

Table 6.5 Numbers ± standard deviation (SD) of breeding Greater Flamingo and their chicks on Sua pan during the 1999-2000 and 2000-2001 wet season. Seasonal chick totals represent estimates of those that survived to fledging.

Date	Colony	Breeding numbers (pairs)	Chick numbers
1999-2000			
Dec 27th	Lesser colonies	1128 ± 54	0
Feb 4th	Lesser colonies & GC1	7241 ± 603	~ 2400
March 18th	GC1 & GC2	12986 ± 727	3845 ± 503
April 25th	GC1 & GC2	8696 ± 341	12411 ± 1099
May 30th	GC1 & GC2	0	16098 ± 1725
Seasonal Total		**23869 ± 1671**	**18498 ± 1725**
2000-2001			
Feb 12th	Lesser colonies	651	0
April 30th	Lesser colonies	0	unknown

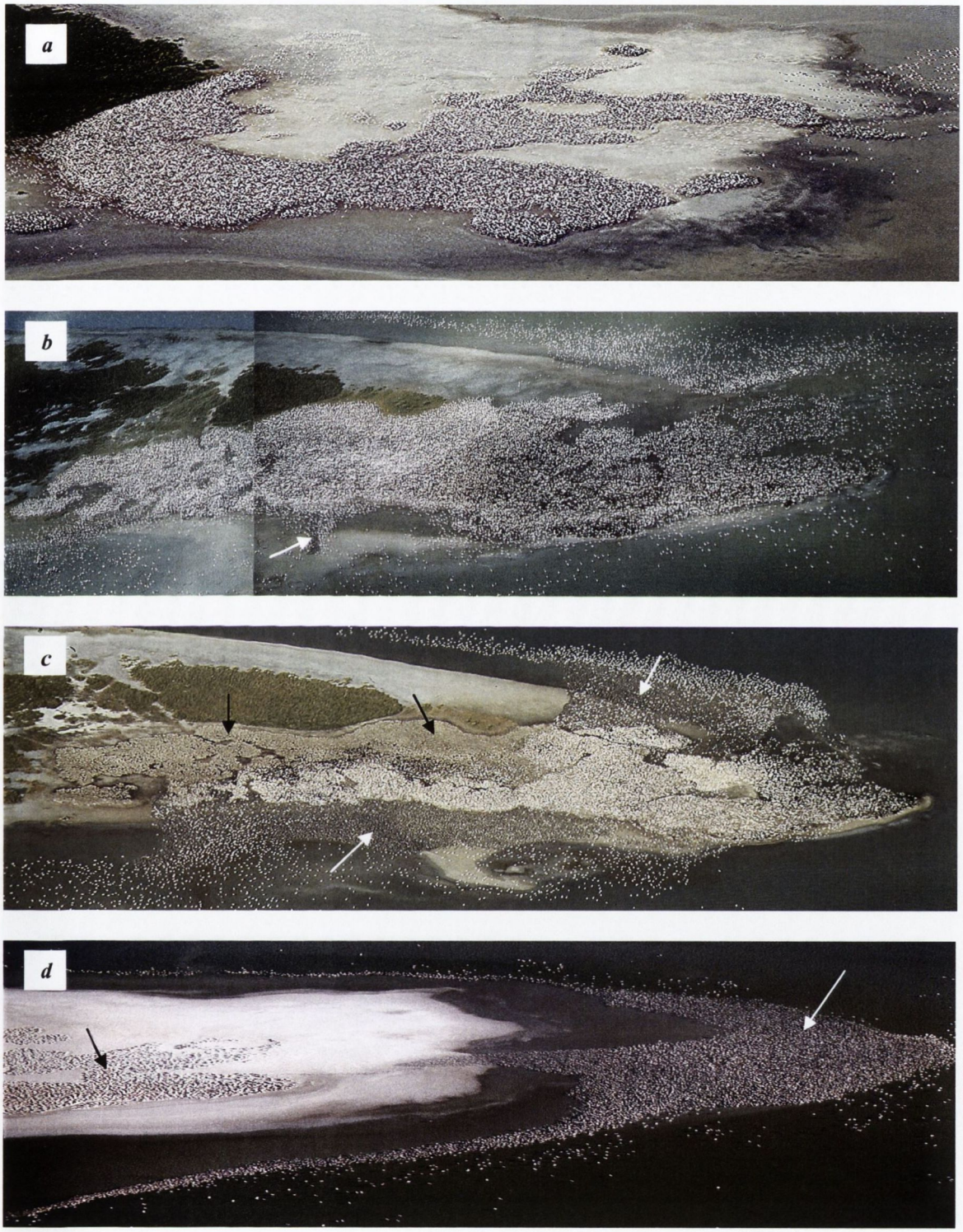

Plate 6.3 Greater flamingo breeding on colony 1 (GC1) during the 1999-2000 wet season, recorded on February 4th (*a*), March 18th (*b*), April 25th (*c*) and May 30th (*d*). White arrows indicate crèches, black arrows empty nests. Colour is exaggerated to define breeding adults and chick crèches.

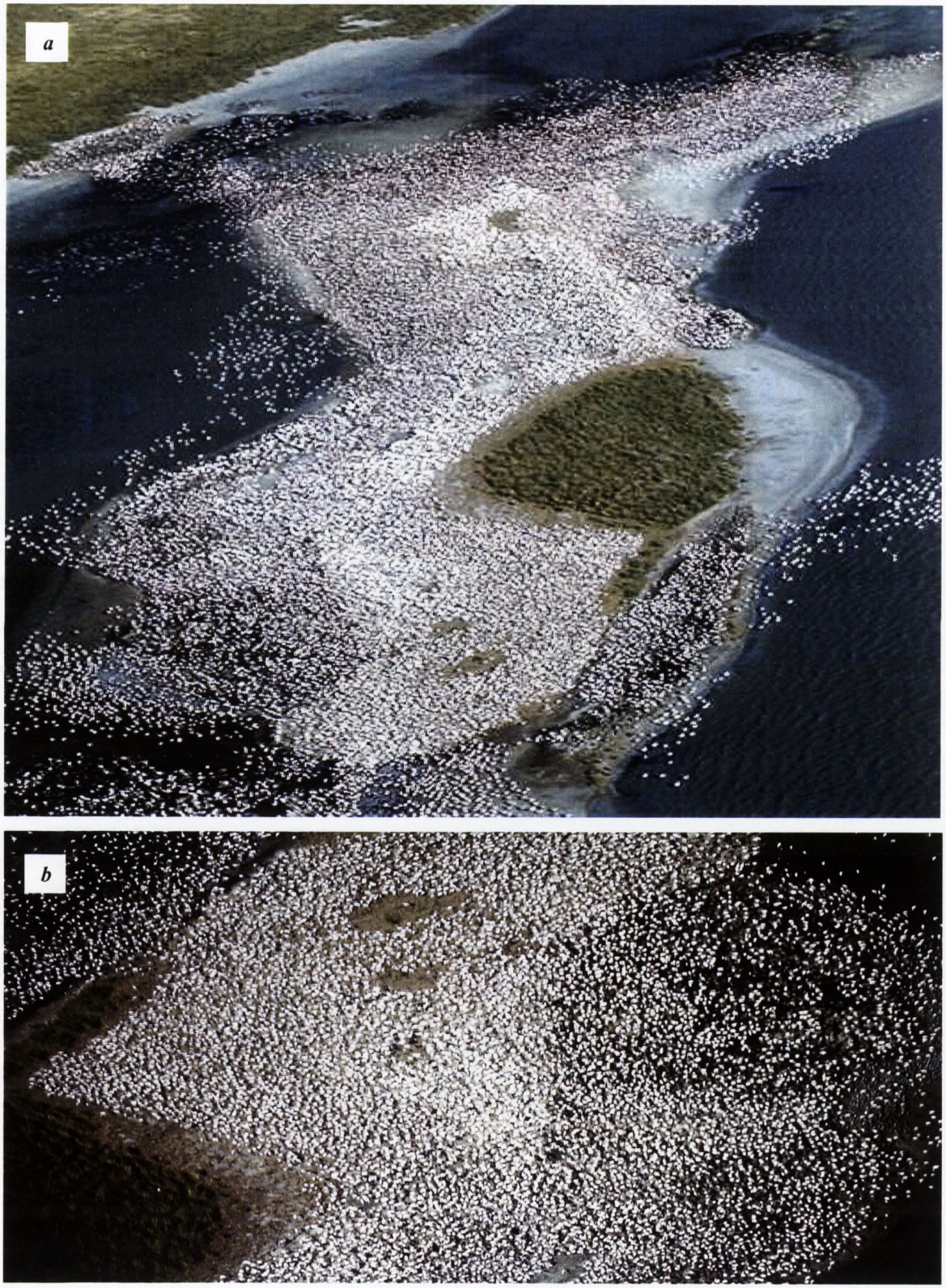

Plate 6.4 Greater and Lesser flamingo breeding on a second island colony (GC2) in April 2000. A white centre represents the Greater flamingo (*a*), which are also larger (*b*).

6.3.2.2 Lesser Flamingo

During a single aerial survey of the south pan on the 2nd of January 1999, a total of 16430 nesting Lesser Flamingos were counted on a large colony built in northwestern area of the south basin (Fig. 6.3). Breeding, however, was only partially successful. The south basin dried up completely by the end of March, forcing the adults to leave thousands of chicks. Large numbers of carcasses, observed scattered across the dry pan some weeks latter, confirmed that many chicks died. Although some chicks fledged and left Sua pan with the adults in late March, it was impossible to say how many. Sightings of small groups of small grey flamingos were reported soon after, on Kamfers Dam, South Africa (Mark Anderson pers. comm.) and Walvis Bay, Namibia (Rob Simmons, pers. comm.). No other breeding by flamingos in southern Africa had been reported that year.

On returning to Sua pan the following wet season, Lesser Flamingos took part in a breeding event that lasted for five months and involved over a 120000 individuals (Table 6.6). On December the 27th, 1999 an estimated 4214 Lesser Flamingos were sitting on nests on the same large colony as the previous year and, already, 1043 chicks had formed a crèche on the edge of the colony. By the 4th of February 2000, an extended aggregation of small colonies contained an estimated 43516 nests. A large crèche and numerous small gatherings close to the nests contained a total of 3849 chicks. Crèche numbers increased to 14120 when the colonies were surveyed on the 18th of March. Nest numbers were, however, very different. Only 5430 nests remained from the 43516 estimated in February and 3927 of them contained incubating adults. Rising water levels washed most of the other nests away and later, thousands of eggs were seen scattered around the colonies. Of those that were forced to abandon their flooded nests, some may have contributed to a growing colony that formed around the Greater Flamingo colony GC2. An estimated 5109 nests, containing Lesser Flamingos, were counted on this colony during the same survey. Estimated numbers on this colony increased to 16557 nests on the 25th April. A few thousand chicks surrounded the nests but it was difficult to distinguish Lesser Flamingo chicks from those of Greater Flamingo. Breeding on the 'Lesser colonies' to the northwest had finished by then and the chicks from the remaining 3927 nests had joined nearby crèches. Owing to a decrease in the numbers of chicks, to 6682, and

considering their age, it was assumed that many of the chicks from the 'Lesser colonies' crèches had already fledged and joined the adults in the feeding grounds. During a survey of GC2 on the 30th of May, large crèches numbering 16133 chicks were observed around the empty colony. According to the proportion of breeding Lesser flamingo on the colony, their chicks made up 82% of the crèche numbers, 13229 chicks. The colony remained surrounded by water until all the chicks fledged. Estimates were that 128574 adults successfully raised a total of 30646 Lesser Flamingo chicks. 86% of the maximum estimated adult population took part in breeding event that produced an estimated 0.48 chicks per breeding pair.

Breeding began again in early December 2000 and by the 12th of February 2001, 12340 nests were occupied on a large Lesser Flamingo colony as before and 2992 chicks aggregated next to the colony. Very dry conditions on and around the colony facilitated high predation by eagles and vultures. Fifteen Lapped faced Vultures, for example were observed on the colony feeding, mainly on chicks, during the February survey. The rains did not arrive that season until March and by the 30th of April breeding had stopped and a total of 8665 chicks were counted in two separate crèches. Flooding from the rains in March were quick to disappear and many of the younger chicks wandered aimlessly around the dry pan. Thousand of carcasses were later found scattered across the pan and it was assumed that approximately half the chicks fledged. In total, only 25% of the population took part in breeding during the 2000-2001 wet season and produced approximately 0.15 chicks per breeding pair.

Table 6.6 Numbers ± SD of breeding Lesser Flamingo and their chicks on Sua pan during the 1998-1999, 1999-2000 and 2000-2001 wet season. Seasonal chick totals represent estimates of those that survived to fledging.

Date	Colony	Breeding numbers (pairs)	Chick numbers
1998-2000			
Jan 2nd	Lesser colonies	16430 ± 823	unknown
1999-2000			
Dec 27th	Lesser colonies	4214 ± 226	1043 ± 127
Feb 4th	Lesser colonies	43516 ± 3404	3849 ± 241
March 18th	Lesser colonies & GC2	9036 ± 597	14120 ± 1310
April 25th	GC2	16557 ± 1283	>6682 ± 720
May 30th	GC2	0	13229 ± 2915
Seasonal Total		**64287 ± 4913**	**30646 ± 4666**
2000-2001			
Feb 12th	Lesser colonies	19340 ± 1291	0
April 31st	Lesser colonies	322	8665 ± 504
Seasonal Total		**19340 ± 691**	**~3000**

6.3.2.3 Flamingo productivity

Greater and lesser Flamingo production during the 1999-2000 wet season was, respectively, 118 and eight times higher than during the 2000-2001 wet season (Table 6.7). Greater Flamingo egg production accounted for an estimated 7% and 23% of production during consecutive seasons, while egg production among the Lesser Flamingo population accounted for 11% and 27% of production during the consecutive seasons. The rest of production comprised the growth of chicks during the 70-day period it took to fledge. Total daily production during this period of chick growth was estimated to be 417 kg d^{-1} during the 1999-2000 wet season. When projected onto the estimated flood area of Sua pan during mid breeding season (April 2000), daily chick productivity was equivalent to 0.056 and 0.07 mg dw m^{-2} d^{-1} for, respectively, Greater and Lesser Flamingo for that period. While total chick production during the 2000-2001 wet season was 1-2 orders of magnitude lower than the previous season, areal daily chick production was similar, estimated to be 0.004 and 0.074 mg m^{-2} d^{-1}.

Table 6.7 Greater and Lesser Flamingo production during the 1999-2000 and 2000-2001 wet seasons. Daily chick production during 70 days of chick growth in parenthesis.

			Chick Production		
Season	**Species**	**Egg P (kg)**	**Total (kg)**	**(kg d^{-1})**	**Total P (kg)**
1999-2000	Greater Flamingo	976.2	12993.0	(185.6)	13,969.2
	Lesser Flamingo	1947.9	16156.6	(230.8)	18,104.5
2000-2001	Greater Flamingo	26.6	91.3	(1.3)	117.9
	Lesser Flamingo	586.0	1581.6	(22.6)	2,167.6

6.3.3 Flamingo diet

6.3.3.1 Greater Flamingo

Crop contents and faecal samples comprised mostly crustaceans. Diet composition varied, however, and the proportion of crop biomass represented by each crustacean group changed as the season progressed (Table 6.8). At the beginning of the season the majority of the crop contents comprised phyllopods, mostly species of anostracan and their eggs. In April and May, the diet included more species and anamopoda contributed a large proportion of total crustacean biomass intake.

Table 6.8 Contents of Greater Flamingo crops and faeces during the 1999-2000 and 2000-2001 wet seasons, showing the proportional biomass in crop samples and the mean proportional abundance in faeces of each crustacean group. Beetles and insect larvae are included under the category 'others' and quantified numerically from the crop samples.

		Proportional contents of crop/faeces				
Date	**site (n)**	**phyllopoda**	**anamopoda**	**copepoda**	**ostracoda**	**others**
Crop						
Dec 24th, 1999		99%	1%			1
Jan 13th, 2000		86%	14%			
Apr 10th, 2000	(2)	15%	59%	9%	17%	2
May 8th, 2000	(2)	61%	37%		2%	9
Faeces						
Dec 17th, 1999	south (4)	96% (eggs)	4%			
Dec 24th,	north (1)	65%	8%	14%	9%	4%
Jan, 23rd, 2000	middle (3)	73%	18%		7%	2%
Mar, 7th	middle (2)	43%	41%	4%	12%	
Apr, 26th	south (3)	33%	77%			
June 14th	south (4)	49%	48%			2%
Aug 3rd	middle (2)	50%	14%		31%	5%
Nov 8th	north (3)	13%	21%	7%	48%	11%
Mar 27th, 2001	south (2)	66%	34%			

6.3.3.2 Lesser Flamingo

Nodularia and diatoms dominated the Lesser Flamingo crop and faecal samples (Table 6.9). Less variation, however, occurred in the respective species compositions and, in general, not much variation occurred between the crop contents and that of the faeces. I was also assumed that the contents in the gut and faeces are what the bird was assimilating. Diatoms and *Spirulina* became abundant at the end of the flood periods, when the Lesser Flamingo were feeding in very shallow water.

Table 6.9 Contents of Lesser Flamingo crops and faeces during the 1999-2000 and 2000-2001 wet seasons, showing the proportional biomass in crop samples and the mean proportional abundance in faeces of each algae and diatom group. Included in the category 'other' were small ostracods and parts of anamopoda.

		Proportional contents of crop/faeces			
Date	**site (n)**	***Nodularia* & *Oscillatoria***	***Spirulina***	**Diatoms**	**other**
Crop					
Dec 5th, 1999	(6)	63%		37%	
Mar 14th, 2000	(1)	74%		26%	
Apr 20th	(2)	52%		48%	<1%
June 2nd	(3)	79%	2%	21%	<1%
June 12th	(1)	67%	1%	32%	
Faeces					
Dec 16th, 1999	north (2)	81%		19%	
Apr 26th, 2000	south (3)	75%		24%	1%
May, 31st	south (4)	59%	13%	28%	
June 14th	south (4)	66%	2%	32%	
July, 11th	middle (3)	83%		15%	2%
July 28th	middle (2)	78%		22%	<1%
Aug 11th	middle (4)	81%		17%	2%
Oct 16th	north (2)	59%		40%	1%
Dec 4th	middle (4)	54%		46%	
Mar 23rd, 2001	north (4)	79%		20%	<1%
Apr 10th	middle (3)	43%	4%	51%	2%
June 1st	north (2)	72%	11%	16%	1%

6.3.4 Flamingo consumption rates

6.3.4.1 Greater Flamingo

Using individual daily consumption estimates taken from the literature, theoretical consumption estimates required to sustain the total Greater Flamingo population on Sua pan varied according to fluxes in the population and the area of flooding (Table 6.10). During the 1999-2000 wet season, a daily consumption of 270 kg DW was estimated for December 1999. Projected onto the lakes of Sua pan total population consumption rates for that month were equivalent to an average of 2.85 mg DW m^{-3} d^{-1} (or 1.42 mg m^{-2} d^{-1}). When the population increased, daily consumption increased to 4.28 tons DW d^{-1} during April 2000, although equivalent volumetric and areal consumption (per m^3 and m^2) were similar to those in December (Table 6.10) owing to an increase in the flood area. Assuming the population was similar to the period between February and April 2000, total consumption remained very similar in June. Consumption rates per m^3 and m^2 were, however, considerably higher (Table 6.10) owing to the rapid decrease in flood area and increase in flamingo concentrations on the remaining area. During the 2000-2001 wet season, total food consumption for the population decreased as the population decreased but, because the flood area was also reduced to approximately half the area of the north basin, population consumption rose to an estimated 32.4 mg m^{-3} d^{-1} and 16.2 mg m^{-2} d^{-1}. Food consumption during the breeding season was, however, double that of estimated normal free existence, 175 g DW d^{-1}. Based on the numbers in the population that took part in breeding during the 1999-2000 wet season, food consumption was double that required by the total population during normal free existence (Table 6.10). With breeding numbers being much lower, additional energy requirements of breeding birds had little impact on total food consumption during the 2000-2001 wet season.

6.3.4.2 Lesser Flamingo

Theoretical estimates of Lesser Flamingo food consumption on Sua pan, based on daily consumption rates in the literature, also varied according to population size and flood area (Table 6.10). Consumption by the population increased by one order of magnitude, from one ton DW d^{-1} in December 1999 to 10 tons d^{-1} in April 2000. As a result of a smaller flood area to total population consumption ratio in December 1999, the volumetric and areal food requirements on Sua pan were much higher than those in April 2000 (Table 6.10). Assuming the population on Sua pan in June 2000 was similar to the mean population of the period February to April, volumetric and areal rates increased again owing to decreasing flood area in all three basins. A highly concentrated population on the last remaining water in the north basin resulted in a very high consumption estimate per m^3 and m^2 in February 2001 (Table 6.10). As with the Greater Flamingo, energy requirements among breeding birds were calculated to be approximately double that of normal free existence (142 g DW d^{-1}). Total food consumption of the Lesser Flamingo breeding population (18.3 tons) was, therefore, almost double that of the total population during normal free existence in April 2000. An extra 2.5 tons DW d^{-1} was required by the breeding population in February 2001 resulting in consumption estimates for the breeding population being approximately half that required for the free existence of the entire population.

Table 6.10 Food consumption rates based on Greater and Lesser population energy requirements needed for free existence and on the higher energy requirements of the breeding populations during the 1999-2000 and 2000-2001 wet seasons. Total estimates for June 2000 were based on average population estimates for February, March and April that year. Consumption rates in mg m^{-2} d^{-1} are given in parenthesis.

	Population Free existence Consumption Rates				Breeding Population Consumption Rates			
	Total (tons/d)		mg m^{-3} flood d^{-1}		Total (tons/d)		mg m^{-3} flood d^{-1}	
Date	Greater	Lesser	Greater	Lesser	Greater	Lesser	Greater	Lesser
20-Dec-99	0.27	1.42	2.85 (1.42)	14.94 (7.47)				
18-Apr-00	4.28	10.2	3.30 (1.65)	7.87 (3.93)	8.35	18.26	6.44 (3.22)	14.08 (7.04)
24-Jun-00	4.41	10	5.29 (2.65)	12.00 (6)				
2-Feb-01	2.95	10.4	32.35 (16.17)	114.10 (57)	0.23	5.49	2.50 (1.25)	60.23 (30.11)

6.3.5 Satellite tracking flamingo from Sua pan

The quality of the PTT transmissions received was very good. 54% of all position data (1906 out of 3546 positions) were of LC 3, LC 2 or LC 1 quality and the majority were, therefore, within 1 km of each PTTs real position. The results that follow only contain position data of this quality.

Owing to exceptional floods, the pans did not dry up in 2001 and the flamingos remained to complete another breeding season. Of the 8 birds that were 'tagged', two Greater and three Lesser Flamingo PTTs were still transmitting at roughly the same location, to the NE of Sua pan: 20° 22′ S, 26 ° 12′ E when the pans finally began to dry out completely in February 2002. The Greater Flamingos (GF *a* & GF *b*) left the pans between the 18th and 20th of February 2002 (Fig. 6.6). On the 20th, GF *a* had moved 170 km west to a small

pan on the western edge of the Makgadikgadi (i): 20° 58′ 40″S, 24° 40′ 08″E (Deg Min Sec). Two days later, on the 22nd, it was located 580 km southeast on a small lake (ii): 26° 07′ 12″S, 25° 49′ 51″E, 5 km from Springbok pan in the western Gauteng provence of South Africa. GF *b* left Makgadikgadi on a westerly course and during the night of the 20th was located 700 km away, flying in the direction of Etosha pan, site (iii): 19° 54′ 39″S, 18° 59′ 13″E, in Bushmanland, northeastern Namibia. Flamingos have been observed stopping at pans close to this location point on numerous occasions and presumed to be transient flocks, en route between Botswana and Namibia (Hines, 1993; Simmons, 1998). Part of this flight (54 km) was tracked continuously for 49 minutes with an estimated average ground speed of 65 km/hr. Etosha pan was dry and therefore unsuitable habitat for flamingos then. On the 22nd of February GF *b* was located on the coast of Namibia, 45 km north of Walvis Bay, 1230 km from Makgadikgadi. On the 26th it had moved south to Walvis Bay (iv): 22° 35′ 24″S, 14° 33′ 14″E.

On the 20th February all three Lesser Flamingos (LF *a*, *b* & *c*) were still on Makgadikgadi. In the weeks following their departure from the Makgadikgadi, we observed a highly dispersed movement (Fig. 6.6). On the 23rd of February LF *a* and *b* were located 930 km SSE on Kamfers dam (v): 28° 40′ 26″S, 24° 47′ 06″E, an important non-breeding site in the Northern Cape province of South Africa. Regular observations of large numbers of flamingos have been recorded on this wetland (summarised in Anderson, 2000*c*). On the 26th and 28th LF *a* then moved 130 km east, to Skoppan (vi): 28° 38′ 31″S, 26° 07′ 30″E and 60 km north, to a small pan (vii): 28° 05′ 38″S 26° 12′ 54″E, near Flamingo Pan. On the 9th of March it flew to another small wetland (viii): 28° 23′ 08″S, 26° 23′ 44″E 17 km south. LF *c*, on the other hand, made its first stop on a small pan, (ix): 21° 17′ 38″S, 25° 22′ 40″E, 130 km south of Makgadikgadi, before flying to wetland (x): 26° 24′ 07″S, 25° 37′ 26″E, near Barbers pan, where it was located on the 4th of March. It was then located on the night of the 6th of March, flying to a wetland in the Lake Chrissie area, site (xi): 26° 14′ 42″S, 29° 05′ 27″E, 160 km east. During this flight the bird flew 90 km in one and a half hours at an average ground speed of 60 km/hr.

Despite observations of flamingos occasionally flying over land by day (e.g. Williams, 1993), we recorded migration in progress only during night-time 'on' periods, supporting the theory that flamingos in Africa fly between wetlands at night (Brown *et al.*, 1982). Later in the year some of the flamingos continued nomadic movements to different locations. GF *a* moved 40 km SSW to wetland (xii): 26° 44′ 02″S, 25° 61′ 53″E, on the 31st of March, where it remained until the PTT stopped transmitting on the 3rd of May. On the 5th of May GF *b* flew 45 km south to Sandwich harbour (xiii): 23° 36′ 33″S, 14° 47′ 21″E. It returned to Walvis Bay again on the 2nd of June and later that month the bird was found dead (with the transmitter attached) on the edge of a salt works pond 38 km north of Walvis Bay, where it was reported scavenged by a Jackal. On the 21st of April LF a returned to Kamfers dam (v). In June and July it continued its nomadic movements, visiting small wetlands (xiv): 28° 18′ 22″S, 26° 10′ 30″E and (xv): 27° 46′ 12″S, 26° 39′ 43″E, before returning once again, to Kamfers dam in August. It remained here until the PTT stopped transmitting in mid-September. On the 10th of May LF *b* had moved 200 km NE, very close to wetland (xv), at 27° 77′ 23″S, 26° 57′ 31″E. The PTT stopped transmitting for a time on the 29th of June. It began transmitting again on the 29th of September and LF *b* had then moved to Lake Nanghul (xvi): 24° 22′ 44″ S, 33° 35′ 20″ E, a perennial freshwater lake in southern Mozambique.

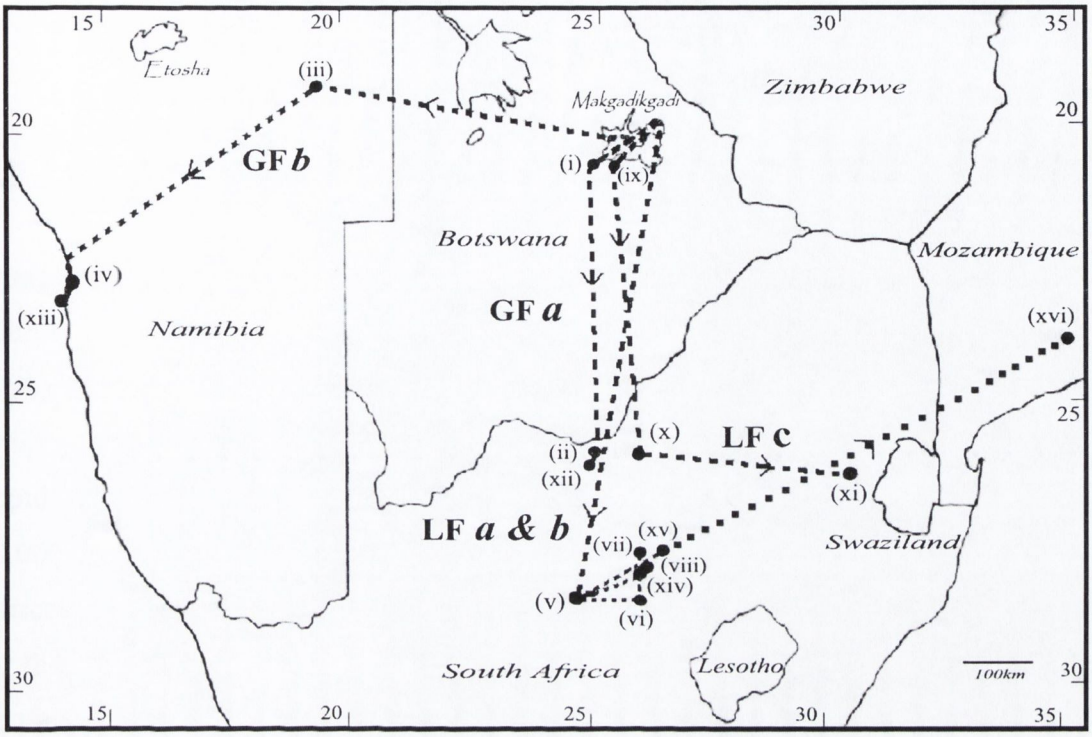

Figure 6.6 The migration of Greater Flamingo (GF *a* & *b*) and three Lesser Flamingo (LF *a*, *b* & *c*) from the Makgadikgadi saltpans to their non-breeding destinations around southern Africa.

6.4 Discussion

6.4.1 Population and biomass densities on Makgadikgadi

From pan-African waterfowl counts carried out bi-annually, the resident Greater Flamingo population in southern Africa has been estimated at between 47,000 (Simmons, 1996) and 55,000 (Dodman & Taylor, 1995). Resident Lesser Flamingos are also estimated to number approximately 55,000 individuals, although a decline in the population of over 20% (matching a similar decline in the total African population) to 40,000 has been suggested by Simmons (1996; 2000). These figures originate from the African Waterfowl Census carried out bi-annually in July and January and do not account for the large populations recorded on both Etosha and Makgadikgadi during years of high rainfall and good breeding conditions. During the 1999-2000 and 2000-2001 wet seasons the Greater Flamingo population matched that of the entire southern African population (Table 6.3). Lesser Flamingo numbers, however, were about three times the southern African population estimates (Table 6.4). Population estimates between February and April 2000 did fluctuate somewhat and this was likely to be the result of a wide dispersal over the entire area of the Makgadikgadi complex, including all of Ntwetwe pan to the west, Nxai pan to the northwest and the hundreds of tiny pans surrounding them. Owing to logistical and cost restraints it was impossible to cover the entire area during aerial surveys. Long flights from breeding colonies to feeding grounds are said to be avoided by breeding flamingos owing to the resulting higher energy costs and reduced feeding time and may influence breeding success and fitness, especially among the younger pairs (Cezilly, 1993; Cezilly *et al.*, 1995). Breeding populations tend, therefore, to spend much of their time feeding close to the breeding colonies. Notwithstanding this, total population estimates for the Makgadikgadi are likely to have been even higher owing to dispersal around the rest of the Makgadikgadi wetland complex. Estimates for the 2000-2001 wet season may also have been underestimates owing to dispersal around the Makgadikgadi during the poor breeding and feeding conditions on Sua pan at the time of the survey. As

they stand, Lesser Flamingo figures still suggest an influx of flamingos from some other region, perhaps East Africa.

Average body weight for Greater Flamingo on Sua pan (3.15 kg), used to calculate biomass densities, was slightly higher than an average of 2.73 kg, recorded by Mendelson & Brown (1988) on Etosha pan and similar to an average estimate of 3 kg for East African birds (Brown, 1973). Similarly, average weight used to calculate Lesser Flamingo biomass density (1.74 kg) also compares with averages of 1.6 kg on Etosha pan (Mendelson & Brown, 1988), 1.76 kg in East Africa (Brown, 1973) and 1.73 kg on Lake Nakuru (Vareschi, 1978). The higher body mass of those weighed on arrival to Sua pan, in December 1999, averaging 2.3 kg, suggests the laying down of large fat reserves by Lesser flamingos for migration to the pans and/or for breeding. Considering the high energy requirements during the breeding season, the importance of this fat, which comprised an additional 32% of average body weight, as an energy reserve may be crucial to the breeding success and long-term reproductive fitness of these birds (discussed further below).

Greater Flamingo biomass densities, which ranged from 15 to 37 mg DW m^{-2} between December 1999 and August 2000, comprised a very small percentage (0.2 – 0.6%) of average areal crustacean biomass on Sua pan of 6.2 g DW m^{-2} (the combined average biomass of the three basins) and an even smaller fraction of the average crustacean production of 10.8 g DW m^{-2} d^{-1}. The biomass density estimate for February 2001 (Table 6.3) was 2.2 % of the average crustacean biomass of 5.6 g DW m^{-2} for that season. Lesser Flamingo biomass density during the 1999-2000 wet season (23 to 54 mg m^{-2}) comprised only a small fraction of the total biomass for primary producers on Sua pan, that ranged between 2.6 g and 44.6 g DW m^{-2} during that season (combined phytoplankton and periphyton biomass from the three basins, assuming fresh weight is five times dry weight (Talling & Lemoalle, 1998) and, when converting volumetric phytoplankton biomass, an average lake depth of 0.5 m for that season). During the 2000-2001 wet season their biomass density comprised 4.8% and 0.8% of the minimum and maximum primary producer standing crops for the season, of, respectively, 5.7 g and 32 g DW m^{-2}

(assuming an average lake depth of 0.3 m on Sua pan when converting volumetric phytoplankton biomass).

Flamingo biomass densities were, generally, similar than those recorded on many of the saline lakes of East Africa. Some lakes do, however, support higher flamingo biomass densities. Vareschi (1978) calculated densities of 12.5 g DW m^{-2} on Lake Nakuru, which comprised 3% of the estimated *Spirulina* standing crop at that time. Tuite (1978) recorded overall biomass densities in some of the more productive lakes as being >80 g m^{-2}, and as high as 755 g m^{-2} where *Spirulina* was the main food source and available at maximum recorded concentrations. The high ratio of food abundance to Greater and Lesser Flamingo biomass densities on Sua pan suggests plenty of food was available for both populations. In order to meet their metabolic energy requirements, however, food consumption rates for each species depended on individual feeding rates and the proportion of the day spent feeding.

6.4.2 Food requirements in relation to population numbers and breeding success

Assuming Greater Flamingo filter approximately 500 l hr^{-1}, assuming 100% filtering efficiency with an 80% assimilation rate (Jenkin, 1957; Vareschi, 1978), individuals feeding for at least 20 hrs a day require a minimum food concentration of 10.25 g DW m^3 to meet their energy costs of free existence. Projected onto Sua pan, assuming an average depth of 0.5 m, the lower limit of food concentration required to meet the energy costs is equivalent to 5 g m^{-2} for a non-breeding flamingo. Because energy expenditure during breeding is almost double that of free existence, the food concentrations required by breeding adults spending only half their time feeding (12 hours) would increase to 36.5 g m^{-3} during the breeding season. On Sua pan this is equivalent to an areal food density of 18.25 g m^{-2}. Crustacean biomass densities from tube samples in the north, middle and south basins during the 1999-2000 wet season averaged 3.5 g m^{-2}, 2.2 g m^{-2} and 0.5 g m^2 respectively and daily crustacean production rates averaged 1.5 g, 5g and 4.3 g m^{-2} d^{-1}.

Average crustacean biomass and production failed to meet Greater Flamingo energy requirements, feeding at the above rates. This assumes that the food requirement model is accurate and crustacean biomass estimates have not been overestimated (Chapter 5). Head moving and stamp feeding behaviour during feeding is, however, thought to increase filtration rates and would therefore increase daily food assimilation at lower densities (e.g. Vareschi & Jacobs, 1984). In addition, while estimated mean crustacean densities in the basin were lower than those required for daily flamingo consumption, maximum densities during the 1999-2000 wet season, particularly during the months March to May 2000 in the north and middle basins, provided plenty of food. Densities of up to 20 g m^{-2} in the north basin and 17 g m^{-2} in the middle basin (Chapter 5) meant that flamingo would need only to feed for 4 to 5 hours in order to meet daily energy requirements. Owing to the highly clumped nature of crustacean distribution flamingos tend to concentrate their feeding efforts in areas of high food densities and where prey is most accessible (e.g. Britton *et al.*, 1986; Arengo & Baldassarre, 1995). As a result, flocks are constantly on the move and vary their feeding sites daily as prey aggregations move and others are depleted. Observations during this study of flocks frequently aggregating into tightly clumped flocks in shallow waters on Sua pan, where densities are likely to be considerably higher than mean values, suggests this to be the case. During the satellite tracking of three Greater Flamingo moving around Sua pan prior to their migration from the pan, during the 2001-2002 rainy season, individuals were located at different sites every two days (every transmission), which supported the likelihood that Greater Flamingos were constantly moving among feeding sites in order to seek out high food concentrations. Consumption rates would, therefore, increase as a result. More importantly, maximum densities during the season (Chapter 5) occur during the breeding season and are high enough to satisfy a breeding birds minimal energy costs if it spent at least nine hours a day feeding. With maximum daily production rates estimated to be approximately 8.5 and 2 g m^{-2} d^{-1} in the middle and south basins, biomass turnover is, however, still slightly below the estimated rate of consumption among breeding adults. Population food consumption was similar during the 2000-2001 wet season (Table 6.10). Average total crustacean biomass estimates in each basin (2.4 g, 2.2 g and 0.6 g m^{-2}) were, again, below the mean areal food concentration required to meet flamingo energy

costs, which were slightly lower (3 g m^{-2}) than the previous season owing to shallow conditions (0.3 m average). Maximum densities could, however, have provided ample food. Unlike the previous season though, maximum densities, occurring in the north (9.5 g m^{-2}) and middle (13.3 g m^{-2}) basins, only just provided areal food concentrations to satisfy estimated reproductive energy costs among breeding adults (equivalent to 10.95 g m^{-2}). While a lack of good breeding conditions (predator protection by flood water) around the traditional island colony in the south basin (Fig. 6.3) cannot be discounted as the reason for poor breeding by Greater Flamingos during the 2000-2001 wet season, it is plausible that lower food abundance and a higher population consumption rate per m^{-2} of Sua pan (Table 6.10) may have been the reason why breeding numbers and breeding success were so low.

Algal biomass density and production on Sua pan also provided important prerequisites to breeding numbers and success among the Lesser Flamingo population. According to experimental evidence, Vareschi (1978) estimated that Lesser Flamingo filter approximately 32 l hr^{-1}. On the basis of this estimate and providing a feeding time of 80% per day, he calculated the lowest algal density that a Lesser Flamingo can effectively feed on to be 140 g DW m^{-3}. His observations of flamingos that stopped feeding at a mean algal concentration of 100 g m^{-3} and evidence of populations in the wild decreasing when the algal densities decreased below this level (e.g. Pennycuick & Bartholomew, 1973; Vareschi, 1978) confirmed that a concentration of >100 g m^{-3} was, in fact, the minimal algal density required to meet minimal energy requirements of free existence. This is equivalent to 50 g m^{-2} on Sua pan assuming a mean depth of 0.5 m. During breeding the food required to meet the higher energy costs of a parent Lesser Flamingo was calculated in this study to be 142 g (2587 kJ) d^{-1}. The lowest algal density required to satisfy this appetite assuming a filtration rate of 31.2 l hr^{-1} (Vareschi, 1978) and an 80% food assimilation rate, was calculated to be 474 g m^{-3}, provided 50% of the day was spent feeding. Phytoplankton density on Sua pan during the 1999-2000 wet season ranged from 0.15 g DW to 10 g DW m^{-3}, calculated by summing minimum and maximum values in the north, middle and south basins (Chapter 4) and assuming 1 g DW ≡ 5 g WW (Talling & Lemoalle, 1998). Maximum concentrations for that season were, therefore, only 10%

of the estimated concentration required for daily consumption during normal free existence and approximately 2% of the concentration required by breeding adults during the breeding season. It was not until May/June 2001, when biomass increased to maximum concentrations of 60 g m^{-3}, that phytoplankton concentration was close to estimated concentrations required for daily flamingo consumption. Vareschi (1978) suggested that flamingos concentrated feeding efforts in areas of wind induced, high algal concentrations and that rapid movements of the head while feeding, greatly increased the filtering rate at lower concentrations. He also calculated a feeding efficiency rate of 80% when Lesser Flamingos were feeding on *Spirulina*, which averaged 120 μ (length) by 25 μ (width) on Lake Nakuru and suggested that feeding efficiency changes according to algae and diatom size. Feeding efficiency on Sua pan may, therefore, be higher owing to the much longer filamentous cyanobacteria (*Nodularia*, *Oscillatoria* and *Spirulina*), which comprised the majority of the diet (Table 6.9). In addition, periphyton biomass was a large and highly concentrated source of food for Lesser Flamingos. Total biomass densities on Sua pan ranged from 2 g to 52 g DW m^{-2} during the 1999-2000 wet season and 11 g to 80 g m^{-2} during the 2000-2001 season (Chapter 4). These densities occurred in very shallow waters where the majority of the flamingos concentrated. When algal densities were low (<100 g m^{-3}) on Lake Nakuru, Vareschi (1978) observed up to 70% of the Lesser Flamingo population feeding on mud flats along the edge of the lake, where, he suggested, more efficient feeding rates may increase daily food consumption. Evidence of their diet comprising mostly species that occur in the periphyton (Table 6.9) and from observations of Lesser Flamingo feeding predominantly close to or directly from the benthic surface during this study suggests that periphyton did, in fact, contribute a large proportion of their diet. Vareschi (1978) calculated that at a filtering rate of 32 l hr^{-1}, flamingos would have to spend approximately 80% of their day feeding in order to filter 140 g m^{-3}. It would be interesting to calculate how much time a Lesser Flamingo would take to scrape and filter the same concentration of algae and diatoms from a m^2 of benthic surface. By concentrating on these productive periphytic layers, that turned over on average between 5.5 and 31 g DW m^{-2} d^{-1} on Sua pan during both study seasons (Chapter 4, g C converted to g organic dry weight by a factor of 2.2, as in Talling & Lemoalle, 1998), food consumption rates per hour were likely to be much higher and may

facilitate the energy surplus required by breeding adults. In fact, thousands of Lesser Flamingo were observed feeding on the mud surface up until the pan was about to dry out completely and long after while Greater Flamingos had already vacated the pan. From feeding trails left on the mud surface by feeding flamingos, they appeared to be 'grazing' the exposed periphytic layer that contained high concentrations of diatoms and cyanobacteria (Chapter 4).

Assumptions based on the relationship between BMR and daily energy requirements may, however, be questionable. Recent statistical studies have revealed significant variation in the relationship between BMR and daily energy requirements in birds, and suggest that the relationship is dependant on whether or not BMR shares the same metabolic pathways as daily activity metabolism, a physiological uncertainty in birds that requires further study (Ricklefs *et al.*, 1996). Tuite (1984) also questions the use of total body mass in calculating metabolic costs in birds. He argued that lean body mass was the more appropriate value to use when calculating BMR based on body mass, considering the varying proportion of fat levels that occur in birds, and estimated this to be 830 g for Lesser Flamingo, from an average body mass of 1400 kg (Tuite, 1978). This being the case, food requirements estimated for both species above would be overestimates and food concentrations required to meet energy demands would be considerably lower.

6.4.3 Breeding success

The Greater Flamingo breeding event of 2000 was an exceptional breeding record of the species in Africa. In 1988 an estimated 42000 - 44000 breeding adults were observed on the island colony GF1 (Fig 6.3) during an exceptional flood and 25000 - 26000 chicks were estimated in a crèche next to the colony later that same year (Hancock, 1990). Apart from mentioning that estimates were calculated from aerial photographs, the report was not clear on the counting methods used. Nonetheless, besides being one of the only records of breeding by Greater Flamingo on Sua pan, it was the largest documented breeding attempt by the species in Africa. The largest breeding attempt recorded in East

Africa occurred on Lake Elmenteita in 1968, when 9500 chicks hatched from 15700 eggs laid during that breeding season (Brown *et al.*, 1973). Indeed, in 21 years of breeding, a total of 56700 pairs laid on Lake Elmenteita (once in Nakuru) and breeding success (chicks raised) averaged 19.3% of eggs laid. The high mortality among eggs and chicks there was attributed to many causes including natural and human disturbances, rising water levels and high predation, particularly by Marabou stork (Brown, 1973). Recruitment on Lake Natron was more successful, estimated at about 48% of eggs laid, although figures were more uncertain (Brown, 1973; 1975). From chick numbers estimated by Hancock (1990) and since then (Tim Liversedge pers. comm.) and from the estimated breeding success during the 1999-2000 wet season in this study, it is evident that breeding by Greater Flamingo on Sua pan, although not as frequent as attempts in East Africa, comprises not only the largest in Africa but the most successful (Table 6.5) and also the largest recruitment rates in Africa. Owing to the isolation and inaccessible nature of the sand spit island and because it was largely unaffected by the rising water levels in March 2000, flamingo breeding on GC1 and GC2 was virtually undisturbed and this accounts for a much higher breeding success on Sua during that season, an estimated 77% of eggs laid, compared with success on East African colonies (19.3% and 48%). In Lake Elmenteita, Brown (1975) estimated that on average 840 chicks per year (4.2%) were being recruited into an adult population of about 20000. If Greater Flamingo breeding on Sua pan occurred only once every five years the average recruitment rate, assuming a population of 50000 and a breeding success rate similar to that in 2000, would be approximately 3700 or 7.4% per annum. In comparison, Greater Flamingo fledglings comprised between 12.6 and 69.6% of eggs laid on a well protected colony in the Camargue, southern France, during seven years of breeding (1984 to 1991) (Cezilly *et al.*, 1995). Post-fledging dispersal from this colony in France, has an important influence on chick survival and subsequent recruitment into the breeding population and is highly dependent on body condition as well as environmental conditions (Nager *et al.*, 1996; Barbraud *et al.*, 2003). If the same is true for Greater Flamingo survival on Sua pan, then chicks reared during an exceptional flood year, when food abundance is sufficient to sustain the population all year round (discussed above), may be in better condition and have a much higher rate of survival compared with individuals reared in years when

flooding is brief and they are forced to migrate with the adults as soon as they fledge, with perhaps less body condition. Adults were also observed feeding chicks that fledged at least four months earlier, which must surely enhance the survival rate of chicks that remain on the pan for longer periods before migrating. In contrast, the lack of breeding and low breeding success during the 2000-2001 wet season may be attributed to the lack of protection and isolation on the island owing to the low rainfall in the early part of the season, although other factors, such as low food abundance during that year (above), may also have had an important inhibiting influence.

The largest concentrations of breeding Lesser Flamingo have been recorded on Lake Natron, where an estimated average of 130000 to 140000 chicks per year were reared between 1953 and 1962 (Brown, 1973). In southern Africa, the largest recorded breeding event prior to this study took place during the wet season of 1971 on Etosha pan, Namibia, where approximately 54000 adults were estimated breeding and breeding success was estimated to be in the region of 37-55% of eggs laid. The Lesser Flamingo breeding attempt during the 1999-2000 wet season was the highest recorded breeding attempt by the species in southern Africa (Table 6.6). Interestingly, owing to the staggered breeding pattern of the breeding attempts, these numbers would not have been calculated from just one aerial survey. Also, the adoption of a Greater Flamingo colony by Lesser Flamingo in March, after they were flooded from their colonies on the open pan surface, had not been recorded before on Sua. Nevertheless, the flooding of colonies in March 2000 was the single most important factor contributing to egg mortality and a breeding success of 48% of eggs laid during that season. It was ironic then that, during the 2000-2001 wet season, a lack of rain meant the Lesser Flamingo colonies were vulnerable to predation by vultures and eagles, which had a greater impact on egg and chick mortality. The most important factor controlling chick mortality during that season was, however, the early drying up of the pan forcing the chicks to trek across the dry pan for weeks in search of water.

6.4.4 Flamingo migration

Flamingo movement from the Makgadikgadi came as a result of the physical disappearance of water forcing them to leave. Thunderstorms may, however, be linked to their arrival on the pans, as suggested by Simmons *et al.* (1998) and similar observations were made during this study and in previous years. The Tswana name for flamingos in Botswana meaning thunder and lightning bird provides some support to this idea. Although none of the tagged birds flew northeast, this study cannot discount the possibilities of migratory connections with East African populations and the evidence for such interchange is still compelling (reviewed in Simmons, 2000; Borello *et al.*, 1998). Indeed Mozambique has been suggested as part of a coastal route north, for inter-connecting populations (Borello *et al.*, 1998). Inspection of the movement of birds suggests that some sites close to the Makgadikgadi (sites (i), (iii) & (ix)) are transient points on longer migration routes, as previously suggested (Hines, 1993; Simmons, 1998), while others are likely important feeding sites for non-breeding populations. The results, particularly those of LF *a*, also show that flamingos are highly scattered and movement is nomadic among the many different wetlands on which they have been recorded (e.g. Borello *et al,* 1998; Anderson, 2000*c*). The majority of sites chosen by the flamingos are located in areas where small predominantly ephemeral pans and dams are highly concentrated (Seaman *et al.,* 1991; Allan *et al*, 1995; Anderson, 2000*c*). Many small ephemeral wetlands throughout southern Africa are, however, vulnerable to disturbance and degradation from, mainly, drainage, domestic waste and agricultural pollution (Davies & Day, 1986; Allan, 1987; Breen, 1991; Allan *et al.*, 1995). Furthermore, most wetlands, including coastal lagoons (like Walvis Bay, Namibia) and many of the dams and other manmade wetlands that often support large flamingo populations, have no or limited protection as conservation sites (Breen, 1991; Allan *et al.,* 1995; Anderson, 2000*c*). The vulnerability of sites that lack a protected status (Ehrlich & Daily, 1993) is a great concern for flamingo conservation as, collectively, scattered and small sites used by these birds are as important in their life-cycle as are the larger sites which afford protection either because of their remoteness (e.g. Sua pan, Magkadikgadi)

or legal status (e.g. Etosha Pan & Kamfers Dam). Research on flamingo habitat ecology and the dynamic use of these habitats by flamingos (e.g. Vareschi, 1978; Arengo & Baldassarre, 1999; Tuite, 2000) suggests that effective flamingo conservation must protect sufficient habitat to secure adequate food availability on a temporal and spatial scale so that quality habitat is always available (Bildstein *et al.*, 2000). Many populations of flamingos inhabit enormous 'ecological neighbourhoods' (Addicott *et al.*, 1987) and understanding the ecology of these populations will require a further research on a regional scale. The results of this tracking project indicate the importance for flamingos of a network of wetland sites across southern Africa and emphasises the need for a reappraisal of wetland protection in the sub-continent.

6.4.5 Conclusions

Flamingo population size and distribution as well as breeding success is greatly influenced by the amount of flooding on Sua pan. While high water levels provide ideal breeding conditions for flamingos in the south basin, this study also highlights the importance of food availability to breeding success of both species. Because the food requirement and energy cost calculations were theoretical estimates and based on some assumptions, there are of course uncertainties in their accuracy and the small sample size of crop and faecal samples exacerbated this problem. Nevertheless, this study examined the important relationship between food availability and flamingo abundance and breeding success, a topic that has received little attention. This is important for the future management of flamingo habitat in relation to their conservation. It is, however, certain that ideal breeding conditions like those on Sua pan during the 1999-2000 wet season, are rare and on such an occasion, appears to draw the entire flamingo population from all over southern Africa. The importance of flamingo food and feeding requirements also has far reaching implications in relation to our understanding of their highly nomadic movements among non-breeding feeding grounds within the sub-continent and beyond. Further studies like this one, combining research on the limnology of flamingo habitat with a study of the feeding ecology and potential breeding success of wetlands that

support flamingo populations in southern Africa, are required to enhance our understanding of the relationship between the important physical, chemical and biological factors controlling food abundance and the maintenance and breeding success of both flamingo populations around the sub-continent.

Chapter 7

General discussion

7.1 Management and conservation implications

Until now, very little was known about the limnology of the intermittent wetlands of the Makgadikgadi and indeed, generally, the limnology of many of southern Africa's temporary saline wetlands have attracted little attention (Mepham, 1987; Allanson *et al.*, 1990; Seaman *et al.*, 1991). The lack of research on the Makgadikgadi's ecosystem is surprising when one considers its importance for biodiversity in the region. Many threatened or endangered bird species feed and breed in its extensive wetlands (e.g. Mundy & Borello, 1990; Simmons, 1996; 2000), and the Makgadikgadi contains species of crustacean that are found nowhere else in the region (Seaman *et al.*, 1991, Brendonck & Riddoch, 1997). It is the most frequently used site by breeding Greater and Lesser Flamingo in southern Africa (Simmons, 1996; 2000) and in years of exceptional rainfall, breeding colonies that form in the south of Sua pan are among the largest in Africa (Parker, 1975; Robertson & Johnson, 1979; Hancock, 1990; Simmons, 1996; 1997; 2000). The Makgadikgadi is, therefore, a wetland of international importance and, only recently, proposals have been put made for it to be designated a Ramsar site, (NCSA, 2000). The consequences of increasing pressure from industry (soda ash mine) and tourism disturbance on the integrity of the Makgadikgadi's ecosystem is, however, difficult to assess without basic knowledge of the physico-chemical factors that control biological community structure, aswell as production within, and interactions between, the different trophic levels of this highly dynamic ecosystem. Although flamingo biologists have made significant contributions to the conservation biology of flamingo species around the world, progress has focused mainly on documenting the natural history of free-ranging populations (Bilstein *et al.*, 2000). This is certainly true in Africa where detailed accounts of their feeding and breeding habits in the past few decades have been few and mostly infrequent (e.g. Berry, 1972; Brown, 1973; Robertson & Johnson, 1979). Most studies on flamingo breeding populations in Africa have been concerned with numbers, breeding success and breeding behaviour, although some ecological studies have concentrated on flamingo food availability and feeding requirements among East African populations (Pennycuick & Bartholomew, 1973; Vareschi, 1978; 1984; Tuite, 1978; 1981). According to Bildstein *et al.* (2000), advances in flamingo biology

are most likely to come from integrated efforts into larger fields of ornithology, ecology and conservation science. In light of this and owing to the severe lack of background knowledge on the ecology of one of their most important breeding sites in southern Africa, this study, the first detailed ecological study of its kind on Makgadikgadi, attempted to document the hydrological and chemical factors that control biological production on Sua Pan, quantify standing crop biomass among the main biological components comprising flamingo food, and relate these to flamingo numbers and breeding success. In doing so, details of the different components of Sua pans ecosystem were identified and quantified. It was hoped that through a detailed study of the ecology of this important flamingo breeding site, a greater understanding of flamingo breeding biology and knowledge essential for the future management and conservation of this important wetland habitat would be ascertained.

The overriding factor determining the existence and production of plants and animals on Sua pan is the amount and duration of flooding. Local climatic conditions are the main determinant of the amount of water input and output (Chapter 2). Its geographical positioning results in elevated temperatures all year round, with high potential evapo-transpiration rates and the seasonal input of water by direct rainfall and river flow is dependant upon the arrival of the inter-tropical convergence zone. Areas of higher rainfall within the catchments of the Nata river can, however, have a large impact on the amount of input onto the north basin and, in years when local rainfall is below average, this can be very important in terms of the period of biological production needed for successful flamingo breeding. The proportion of catchment rainfall, flowing onto the pan as river discharge is, however, low. Ground water table level and the number of wells and dams in the catchment can have large impacts on proportional river discharge (Yair & Lavee, 1985; Shaw, 1994). Standing water ion concentration comprises variable combinations of ions from various origins (Kilham, 1971; Eugster & Hardie, 1978; Williams, 1998). On Sua pan, the proportions of each are dependant on the hydrological regime of each basin, which varies both spatially and temporally (Thomas & Shaw, 1991). High sodium chloride and calcium bicarbonate dissolution on the pan surface gives rise to high pH and saline conditions on Sua pan (Chapter 3). Not many species of

algae and crustaceans can survive in these temporary saline conditions (Hammer, 1986; Williams, DD., 1987; Green, 1993; Williams *et al.*, 1990, 1998) and algae and crustacean richness was, therefore, low at high salinities in the middle and south basin (Chapter 4 & 5). During a large flood, such as occurred during the 1999-2000 wet season, salinity varied widely within and among basins owing to the differences in the proportions of ionic contribution (Chapter 3). This allowed a greater range in conditions, under which algae and crustaceans can exist (Cholnoky, 1966; Hecky & Kilham, 1973; La Barbara & Kilham, 1974; Green, 1986; 1993). Species richness was, therefore, highest in the less saline waters of the north, where *Euglena* and single celled species of green algae and *Chroococcus* provided food for small herbivorous crustaceans like *Daphnia*, that would otherwise be limited by food availability and high salinity and temperatures (Chapter 5). While algae and crustacean richness was generally low, abundance on Sua pan indicated it to be one of the most productive shallow tropical lakes in Africa. This was attributed to the high concentrations of nutrients in its shallow waters, originating from inflowing rivers, a high input and rapid recycling of nutrients by flamingos, and a high rate of nutrient regeneration from detritus and sediment in warm shallow waters (Chapter 3).

Flooding volume controls the area of flooding and, because the pan is so flat, with little gradient to the sumps, high seasonal rainfall causes extensive flooding that covers a high proportion of the pan in shallow water. As a consequence, a large proportion of, and in some cases, the complete water column lies within the euphotic zone and large areas of the benthic surface are illuminated. Other studies have found that very shallow lakes are more efficient at converting available nutrients into phytoplankton biomass owing to the constant and sufficient underwater light climate (Nixdorf & Deneke, 1997). Shallowness in lakes affects quantitative relationships with nutrients and salinities and flux rates per unit surface area: increased surface energy and CO_2, O_2 and N_2 exchange; increased heat distribution and higher evaporative loss of water, with associated concentration of salts and nutrients; and increased sensitivity to wind generated turbulence and changing turbidity, with associated changes in surface light attenuation and depth irradiance (Dumont, 1992; Talling, 1992; 2001). Regular mixing of the water column in shallow waters also contributes to a stable and near optimum light-dark rhythm resulting in very

high primary production rates (Allanson & van Wyk, 1969; Kirk, 1983; Harding, 1997; Talling & Lemoalle, 1998). While the waters of Sua pan experience conditions favourable for primary production (above) owing to its shallowness, the high phytoplankton and periphyton production recorded in this study (Chapter 4), could not, however, have occurred without a large source of nutrients. One of the most important factors controlling the high production rates can, therefore, be attributed to the high concentrations of phosphorus, nitrogen and silicate (Chapter 3). Total phosphorus, for example, was similar to some of the highest concentrations recorded among shallow saline lakes in East and central Africa (Talling & Talling, 1965; Moss & Moss, 1969; Vareschi, 1982). High nutrient concentrations may be the result of long-term continuous input of organic and inorganic forms from the surrounding catchment that accumulated over the millennia. Rapid recycling of detritus in the sediment by bacteria and a rapid turnover of biomass by crustaceans and the flamingos, ensured that high concentration of nutrients needed for rapid production were available in suspension. Total nitrogen was also high, although the amount of available nitrogen on the pan, in the form of nitrate, was unknown (Chapter 4). This nutrient is limiting in other African shallow saline lakes (e.g. Moss, 1969; Moss & Moss, 1969), but this system is more likely to be light limiting owing to the large organic and inorganic turbidity and self-shading by large concentrations of cyanobacteria. Large amounts of organic carbon in the form of detritus in suspension and on the sediment surface are rapidly recycled in such environments (Talling & Lemoalle, 1998) and provide a large source of carbon. Direct use of HCO_3 by algae as a source of carbon in other shallow saline lakes (Ganf, 1972; Talling *et al.*, 1973; Vareschi, 1982) suggests that the high concentrations of HCO_3 found on Sua pan (Chapter 3), also ensured high photosynthetic potential. An abundance of algae and detritus provided plenty of food for the crustacean community, while consistently high water temperatures encouraged rapid growth and production rates (Chapters 5). An abundant source of food was, therefore, available for higher order consumers, mainly Greater and Lesser Flamingo that fed on, respectively, the crustaceans and algae on Sua pan. Flamingos are among the most important consumers of microscopic plants and animals owing to their highly efficient filter feeding (Jenkin, 1957; Bildstein *et al.*, 1993; Zweers *et al.*, 1995) and in shallow temporary lakes, where fish are largely excluded, are

almost alone among vertebrates as the dominant consumers of this abundant food source. Large areas of shallow productive waters are ideal conditions for feeding flamingos (Kear & Duplaix-Hall, 1975; Brown *et al.*, 1982; Britton *et al.*, 1986) and have been reported to contribute enormously to some of the highest flamingo concentration in Africa (e.g. Vareschi, 1978, Tuite, 1978; 1979). Flood volume and resulting lake area, depth and flood period has also been shown in this study to play an essential role in the success of breeding by large numbers of both flamingo species (e.g. Brown, 1959; 1973; 1975, Cezilly *et al.*, 1995; Simmons, 1996). The amount and period of flooding on Sua pan had a large impact on the number and breeding success of both Lesser and Greater flamingos during the study period and was consistent with the amounts of total biomass and production by, respectively, the primary and secondary producers (Chapter 6).

7.2 The food web

The biological components included in this study comprised some of the major components among the trophic levels within the ecosystem of Sua pan: the algae and diatoms (primary producers), crustaceans (primary consumers), Lesser flamingo (primary consumers) and Greater flamingo (secondary consumers). Owing to its temporary nature and, consequently, its highly dynamic hydrological and chemical regimes, the food chain representing material and energy transfer between trophic levels is relatively simple (Fig. 7.1). While autotrophic primary producer biomass, in the form of algae were estimated in this study, bacteria and protozoans, recognised as major contributors to primary production in other African shallow saline lakes (Wetzel, 1995; Talling & Lemoalle, 1998), were not quantified. The role of bacteria and detritus for material and energy flux within the ecosystem of Sua pan is likely to be considerable. Detritus may also comprise a large proportion of food source for crustaceans. Apart from the north basin, during exceptional flooding, fish were not found and the majority of the primary and secondary consumers comprise Lesser and Greater Flamingos. The top predators comprise Jackals, Hyaenas and raptors. Predation by the land predators was opportunistic and appeared

highest on juvenile birds, while Fish Eagles and Lapped-faced Vultures were among the raptors most frequently observed feeding on adults and chicks.

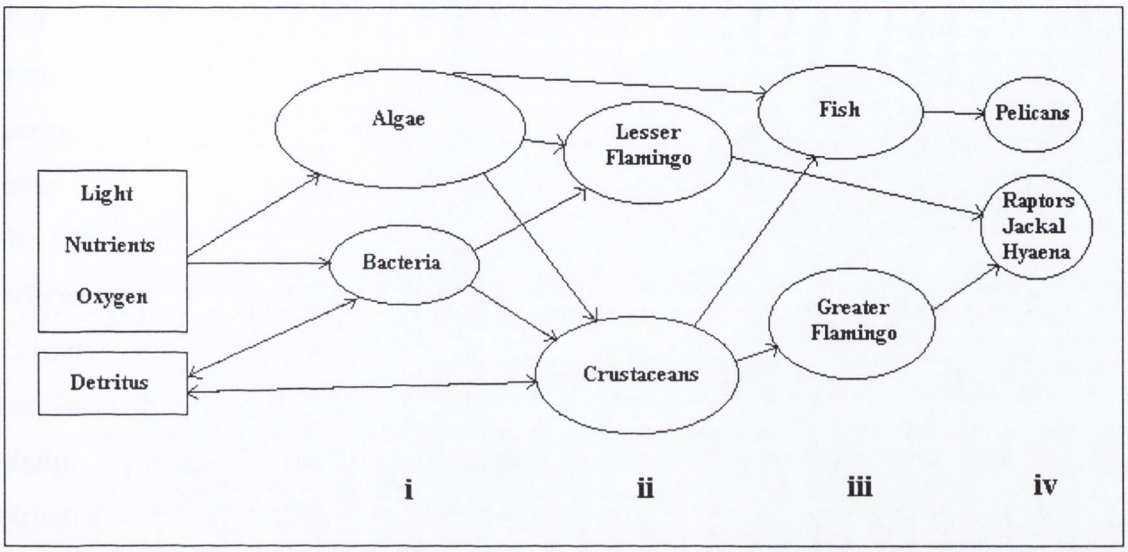

Figure 7.1 Simple food chain of the main components that make up the biota of the aquatic saline ecosystem on Sua pan, making up the primary producer, and primary, secondary and tertiary consumer trophic levels (i to iv).

7.3 Trophic structure

The flow of material and energy between trophic levels has been illustrated for a number of African lakes using 'pyramid' diagrams (Hecky, 1984; Talling & Lemoalle, 1998; Irvine *et al.*, 2001). Ignoring the contributions from detritus and bacteria and the loss of energy to detritus and respiration, transfer efficiencies of energy among trophic levels can be calculated from biomass and production pyramids of Sua pans' biota (Fig. 7.2). Biomass densities per unit area and areal production rates are seasonal averages. The proportion of each component in the higher trophic levels may, therefore, have changed considerably during the flood periods. Based on areal biomass averages, phytoplankton and periphyton algae and diatoms comprised a large base during both wet seasons, with much reduced areal biomass among primary, secondary and tertiary consumers. This is consistent with other highly productive shallow saline lakes in Africa, such as Lake

George and Nakuru (Hecky, 1984; Vareschi & Jacobs, 1985). Alternative sources of organic matter and energy in the form of detritus and bacterial production may, however, have increased this base considerably. A higher primary producer base during the 2000-2001 wet season represents the abundant periphyton community during the shorter flood periods in the middle and south basins in addition to an increase in the phytoplankton and periphyton biomass in the north basin (Chapter 4). Because energy conversion efficiency from the primary producer base level to the top predators is reduced with an increase in the number of conversion steps (number of trophic levels), simple systems are more efficient at converting primary production to the higher trophic levels (Talling & Lemoalle, 1998). Potential transmission of biomass energy over fewer conversion steps on Sua pan likely results in increased energy conversion efficiency through the food chain. Probably the most detailed and comprehensive studies of any African lake trophic structure was that carried out by Irvine *et al.* (2001) on the pelagic ecosystem of Lake Malawi, where most of the energy from the primary producer level flowed through three zooplankters. They found that ecological 'pyramids' based on biomass were somewhat 'topheavy' owing to the accumulation of standing biomass among zooplanktivorous fish in the fourth trophic level, but that those based on production conformed to the expected pyramid shaped trophic model. Production achieved at different trophic levels on Sua pan gave very different production ratios between adjacent trophic levels (Fig. 7.2). The ratio of secondary production to primary production during the 1999-2000 and 2000-2001 wet seasons was, respectively, 60% and 6%. A value of 10 - 15% is often quoted as typical for a production ratio between two adjacent trophic levels (Talling & Lemoalle, 1998). The trophic efficiency calculated between herbivorous zooplankton and phytoplankton in Lake Malawi was calculated for two years to be 7.6 and 5.3% (Irvine *et al.*, 2001). In Sua pan very high trophic efficiency is, therefore, suggested during the 1999-2000 wet season. The majority of primary consumer production comprised crustacean production, even though the proportion of primary production consumed by Lesser Flamingo, with a conversion efficiency estimated to be about 80% (Kendeigh in Pennycuick & Bartholomew, 1973), was likely to be much higher than that consumed by crustaceans (Chapter 6). Similarly, production by crustaceans (copepods) on Lake Nakuru was two orders of magnitude higher than that in the Lesser Flamingo population, even though the

proportion of primary production consumed by Lesser flamingo was double that consumed by copepods (Vareschi & Jacobs, 1985). Conversion efficiencies on Sua are also likely to be overestimates owing to the fact that detritus contributes a considerable proportion of consumption among the anostracans and *Moina* crustaceans, which comprised large proportions of crustacean production during both seasons. Potential secondary production is, therefore, not controlled by changes in primary production and food supply. Notwithstanding this, there appeared a large decrease in the conversion efficiency during the 2000-2001 wet season and this may be owing to the reduced proportion of crustacean production as a result of a shorter flood period in the middle and south basins compared with the rapid periphytic growth on the benthos in those shallow water conditions. The ratio of secondary consumer (Greater flamingo) to crustacean production was negligible (< 0.001%) during both seasons, although high Greater flamingo consumption rates accounted for most, if not all, of total crustacean production (Chapter 6). In the north basin, the transfer of material and energy through fish (both primary and secondary consumers) is uncertain, although during the 1999-2000, an estimated 800 pairs of Great White Pelicans (*Pelecanus onocrotalus*) were observed breeding in the north basin. Vareschi & Jacobs (1984) estimated production among breeding Pelicans to be 48 g DW d^{-1} per chick during the 70 days it took to fledge. In the north basin this converts to an estimated production by the breeding population of 0.06 g m^{-2} d^{-1}, during 70 days in April 2000, which was considerably higher than average production by Greater and Lesser flamingo (Fig. 7.2).

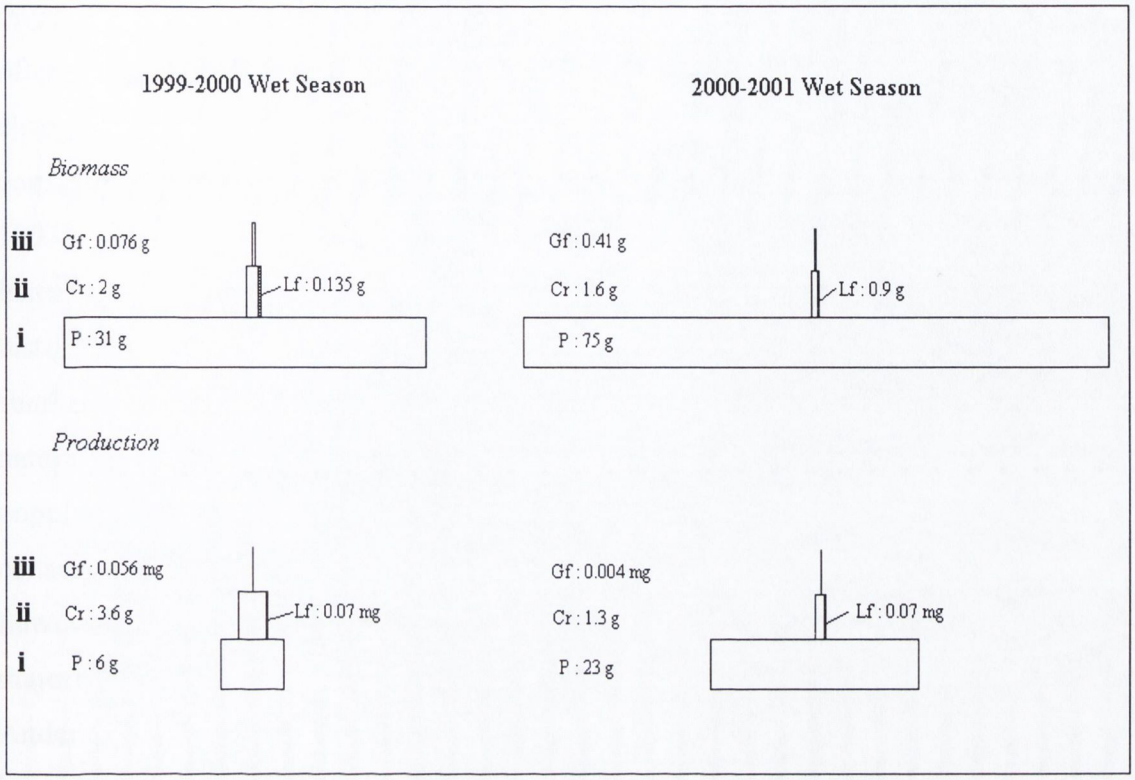

Figure 7.2 Pyramids of biomass (g DW m^{-2}) and daily production (g DW m^{-2} d^{-1}) among the major biological components in Sua pan, algae and diatoms (trophic level i), crustaceans (trophic level ii), Lesser flamingo (trophic level ii, shaded area on right), and Greater flamingo (trophic level iii), during the 1999-2000 and 2000-2001 wet seasons.

7.4 Current issues of saline lake conservation

Saline lakes in arid and semi-arid regions worldwide, most of which are small and shallow and perhaps ephemeral (Hammer, 1986; Williams, 1998), are widespread and numerous (Williams, 1996; 1998) and provide an important component of inland aquatic environments in these regions. Williams (1972; 1981; 1986; 1993), Collins (1977) and Hammer (1978*a*), in particular have drawn attention to the ecological interest and values of saline lakes. Their relative homogeneity of habitat, smaller number of species and simplicity of trophic relationships facilitate comprehensive ecological studies and aid in the understanding of important trophic interactions within aquatic ecosystems.

Physiological interests lie in the nature of numerous adaptations to the stresses of life in often highly saline and hostile environments. Their sensitivity to climate and tectonic change has encouraged strong palaeo-limnological interest also. Saline lakes are also of considerable economic importance in an otherwise undeveloped region (Williams, 1988; 1993). Williams (1986; 1993) stressed the lack of limnological knowledge on saline lakes, especially in arid and semi-arid environments in the southern hemisphere, owing historically to lack of interest, accessibility and economic value. The same is true in southern Africa, where large and small endorheic wetlands provide an important regional natural resource aswell as an important habitat network for the southern African flamingo population (Allan *et al.*, 1995; Anderson, 2000*c*; Breen, 1991; Seaman *et al.*, 1991). The conservation of many of these saline lakes and ephemeral pans around southern Africa is, however, of growing concern owing to the lack of formal, effective protection of the majority of these sites that are under increasing threat (Davies & Day, 1986; Allan, 1987; Anderson, 2000*c*; Breen, 1991; Allan *et al,* 1995). Future long-term monitoring of the limnological status of these wetlands in southern Africa is essential, not only for their effective management on a local and national scale, but to facilitate the development of comprehensive sustainable management and conservation policies on a regional scale and ensure the integrity of an important natural resource and networking habitats for flamingos in the sub-continent.

7.5 Flamingos and saline lake conservation

One of the most mysterious and spectacular of all the birds, flamingos portray a sense of both beauty and robustness. A shocking pink and crimson-red colour, together with their fragile shape and elegant posture, contrast with an incredible ability to survive in some of the hottest and most saline environments on the planet. An oddly shaped yet highly specialized bill has bound them to a life solely dependent on filtering microscopic organisms from their predominantly saline water habitats. Being one of the most gregarious of all the birds, they do so in large flocks and at their most abundant, they are truly one of the most amazing natural spectacles in Africa. Everything about a flamingo

appears to maximise their ability to feed on microscopic plants and animals (Jenkin, 1957; Bildstein *et al.*, 1993; Zweers *et al.*, 1995). In fact, so close is their link to this ancient food chain, it is their prey that gives flamingos their characteristic pink colour. Carotenoids present in the crustaceans and, more so, in the algae eaten by flamingos are converted to feather pigments in the flamingos' liver and are incorporated into growing feathers (in Kear & Duplaix-Hall, 1975).

For centuries, man has marvelled at the flamingos unique attributes and wanted to know more about them and their habitat. Ironically, while the harsh and inaccessible nature of the environment in which flamingos live, has allowed them to exist relatively undisturbed, it has also impaired our understanding of them and in some cases, rendered research on them almost impossible (Brown, 1973; Kear & Duplaix-Hall, 1975). However, these remote sites are no longer inaccessible and the flamingos are no longer isolated. Today flamingos often face severe threats and disturbances when they attempt to breed (Bildstein *et al.*, 2000). Such is the case on Sua pan. Brown (1973; 1975) was the first to emphasise the threat from low flying aircraft, which can cause immense stress to the breeding colonies. Adults flee from their nests to avoid possible danger, leaving eggs and chicks exposed and sometimes knocking eggs off nests. Unknowingly, self-drive tourists attempt the impossible and try and cross the dangerous mudflats, threatening the flamingos isolation and, in doing so, carve up the pan and encourage encroachment by grass. The migration routes the flamingos take to and from the colonies are no longer safe. Man has erected obstacles in their flight path, in the form of power-lines and veterinary fences. Their habitat too is slowly being encroached upon by industrial and tourism activities.

The use of particular species or taxa as symbols or 'flagships' has been adopted by a wide range of organisations and agencies as a means of engaging and informing selected audiences about conservation issues and efforts to combat habitat degradation (Dietz *et al.*, 1994, Bowen-Jones & Entwistle, 2002). This is of particularly importance when the economic returns from such an attractive natural resource plays a vital role in the local economy. Places like Lake Nakuru in East Africa host up to a million Lesser flamingo

and attracts thousands of visitors to its shores each year, each contributing to a multi-million dollar tourist industry. The protection and conservation of flamingos has far-reaching effects on the conservation of their highly dynamic ecosystems too. This has been illustrated at Sua Pan, where a number of measures have been taken to protect the flamingos. This has helped promote the protection of other bird species and wildlife in the area in addition to a greater overall awareness and understanding of the environment and its inhabitants. Power lines have been rendered safe from bird collisions using florescent light bulbs placed on the lines. Projects aimed at rendering some of the dangerous vet fences safe, using home made reflectors, have been carried out by children from the local primary schools. Similar efforts have been taken by local industry (Botswana Ash (Pty) Ltd.) and tourism to insure the integrity of the pan is protected for the good of the flamingos and the rest of its inhabitants. The reaction is by no means complete and indeed it needs to be continuous. In order to be pro-active, however, research like that carried out in this study will highlight the need for important monitoring of basic habitat ecology and to implemented effective management strategies in order to ensure the conservation and future integrity of flamingos habitat on the Makgadikgadi and places like it around southern Africa.

7.6 Summary

The saltpans complex of the Makgadikgadi are a relic of a large and ancient inland lake that once covered most of contemporary northern Botswana. Today remnants of that lake exist in the form of one of the largest saltpan complexes on earth. Two large salt flats, Ntwetwe and Sua Pan, covering approximately 16000 km^2, make up the majority of what might now resemble a portion of that ancient lake. These predominantly dry and desolate mudflats are seasonally inundated in the rainy season and, depending on the amount of rainfall, are transformed into vast shallow saline lakes. Sua Pan, the lowest part of the saltpan complex, is the 'sump' of a large inland drainage system, with a combined seasonal input of water from five inflowing rivers, the Nata, Semowane, Mosetse,

Lepashe and Mosupe. The local semi-arid climate renders the area dry for most of the year and heavy seasonal rains depend on the arrival of the inter-tropical convergence zone. Rainfall fluctuates from year to year, around an average of 450 to 500 mm, making inundation highly variable and, more often than not, water on the pan dries up by the end of the rainy season. However, with above average rainfall the pan can be converted into a vast saline lake that can last for the entire year. On such occasions Sua Pan and the rest of the Makgadikgadi becomes one of the most important wetland ecosystems in southern Africa and attract thousands of Greater and Lesser flamingos from all over southern Africa to feed and breed in its shallow waters.

The first heavy thundershowers of the rainy season contribute to standing water on the pan and shallow lakes begin to form. A large amount of river discharge enters the pan from the East, particularly from the Nata River, although during the exceptional rains of 1999-2000, the rainfall falling directly over the pan contributed more water than river discharge. Although the input of ground water is unknown, it may play an important role in Suas hydrological regime. As if in an instant millions of microscopic flora emerge comprising phytoplankton and periphyton associations (often occurring as dense benthic mats) of diatoms and cyanobacteria. Filamentous cyanobacteria species, *Nodularia*, with *Oscillatoria* and *Spirulina* contribute to community abundance in, respectively, deep and very shallow conditions. *Navicula* and *Nitzschia* were the dominant diatoms and were most abundant in very shallow water and on exposed mud. Phytoplankton abundance and productivity on Sua pan varied considerably among the three basins and within each basin over the flood periods of both seasons. Maximum abundance and productivity rates were similar to those in some of the most productive lakes in Africa. This was attributed to a combination of physical and chemical factors that influenced favourable light, temperature and nutrient conditions, specifically: lake morphology, which influenced water depth and area and provided a source of sediment derived turbidity and nutrients; climate, which controlled seasonal variation of light, temperature, and evaporation rates; geochemical and evaporative concentration of salinity and pH, which controlled species diversity and abundance aswell as CO_2 availability; turbidity, which controlled the depth of light incidence, determined the euphotic zone, and increased nutrient availability; and

wind, which controlled turbidity, nutrient regeneration and probably CO_2 uptake. Some of the algae provided food for various species of small invertebrates. Small crustaceans hatched out from eggs that lay dormant during long dry phases and dominated the zooplankton and the majority of the zoobenthos. Although predatory beetles and insect larvae were found, their contribution to invertebrate abundance and secondary production are unknown. Species diversity among the crustaceans was generally low, but varied according to salinity. The most abundant species were *Branchinella spinosa*, *B. ornata*, *Moina belli*, *Lovenula africana* and *Limnocythere tudoranceai*, while *Daphnia barbata*, *Leptestheria striatoconcha* and *Sclerocypris exserta makarikarensis* occurred less frequently or were abundant for short periods of time. While abundance and production also varied according to a combination of chemical and physical factors, total standing crop biomass and secondary production among the most abundant crustaceans were similar or greater than some of the most productive saline lakes in tropical and sub-tropical Africa (Burgis, 1974; Gras & Saint-Jean 1983; Vareschi & Jacobs, 1984; Mengestou & Fernando, 1991).

Thousands of Greater and Lesser flamingos sense when conditions are good on Sua and migrate from all over southern Africa to feed and breed; their arrival is remarkably well synchronised with the beginning of flooding. The Greater flamingo diet comprised mainly the most abundant crustaceans. Similarly, the diet of the Lesser flamingo comprised the dominant algae and diatom species. During the 1999-2000 wet season, Greater and Lesser flamingo populations reached a recorded maximum of, respectively, 57800 and 149400 individuals, exceeding totals estimated for both population in southern African. During that year 47600 Greater Flamingo raised 18500 chicks, one of the most successful breeding seasons ever recorded in Africa, and 128000 Lesser flamingo raised 30600 chicks. Numbers declined somewhat during the following season owing to less flooding and flamingo dispersal around the Makgadikgadi complex and breeding was only partially successful. Although total food abundance was very high, feeding efforts appeared to be concentrated at sites where food was highly concentrated in order to satisfy the high consumption rates calculated in this study. With elevated food requirements during the breeding season, an abundant food supply close to the breeding

site was recognised as a very important factor in breeding success and the later survival of flamingo chicks. Using modern satellite tracking technology, individuals of each species were tracked during their nocturnal migrations from the pans back to their non-breeding sites, which were scattered throughout southern Africa. Movements were not only highly dispersed from the pan but subsequent movements around numerous large and small wetlands highlighted their nomadic behaviour and a dependence on a network of wetlands for food during the winter (non-breeding) season.

7.7 Future Research recommendations

While many of the components of Sua pans ecosystem were included in this study, some important aspects of the physical, chemical and biological components have been omitted or given little attention. Future research on the following subjects would add to the overall understanding of the Makgadikgadi and intermittent wetlands ecosystems like it:

1. it was very difficult to measure the contribution made by the smaller rivers to net water gain on the pain and a lot more time and effort is needed to quantify the flash flood discharge volumes in order to do so;

2. water gain from, and subsequent loss to, the groundwater table on Sua pan may have an important influence on the hydrological regime, as well as contributing considerable amounts of salinity to the pan surface waters;

3. increasing demands for potable and irrigation water in the river catchments may require a detailed assessment of the annual rate of use from groundwater and dam reserves, particularly in the Nata river catchment, in order to determine its impact on river discharge onto the pan;

4. detailed experiment analyses of primary production, using light-dark bottle experiments, would confirm primary production among the phytoplankton and

further advances in quantifying periphyton community production would facilitate production estimates of an important primary producer community on Sua pan and very shallow lakes like it;

5. the role of bacteria and perhaps protozoans as an important component of the primary producer trophic level in temporary saline lakes need to be determined;

6. similarly, the role of detritus in the flow of energy up the trophic levels, through crustacean detritivores needs further attention. Such studies could be carried out by traceable isotope experiment;

7. growth and production rates among species identified in this study, such as the conchostracan and the *Moina* species and the ostracods, are rare in the literature and require further study in order to accurately determine their importance in the food web of such shallow saline and often ephemeral systems;

8. the contribution to secondary production and the flow of energy up the food chain made by insect larvae and the species of predatatory beetles would also be beneficial;

9. the Makgadikgadi complex is vast and, like Sua pan, its chemical and biological composition is likely to be varied both spatially and temporally and future research may include other areas such as Ntwetwe pan and some of the many smaller pans that are an integral part of the Makgadikgadi wetland ecosystem;

10. further experimental studies of food consumption and feeding rates by Greater and Lesser flamingo, combined with studies of food availability, its variable concentrations and the localised movements of flamingos, would reveal much more about food requirements and optimal foraging behaviour among flamingos in their natural feeding and breeding habitats;

11. experiments using exclusion areas would help determine the top-down control of flamingos on nutrient loading and turnover as well as their effects on the algae and crustacean composition and abundance in this ecosystem and ones like it;

12. Diurnal measurements of Ph and oxygen levels would also reveal a lot about the biological activity and its control on the chemistry of the lakes' waters; and

13. long-term monitoring of the chemical and biological status of flamingo habitat on a regional scale, using remote sensing methods to determine the hydrological state of many small and often temporary wetlands, would be enormously beneficial to our understanding of inland wetland ecology in southern Africa. This would lay the foundations on which to base future research, local management efforts and effective conservation strategies that would help ensure the integrity of small and medium sized wetland habitat around the sub-continent.

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