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ECOLOGICAL SIGNIFICANCE OF BLUE-GREEN ALGAL MATS IN THE DAMPIER MANGROVE ECOSYSTEM

Department of Conservation and Environment
Perth, Western Australia

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THE ECOLOGICAL SIGNIFICANCE OF BLUE-GREEN ALGAL MATS IN THE DAMPIER MANGROVE ECOSYSTEM

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ABSTRACT

This study examined blue-green algal mats on salt flats behind mangroves in the Dampier Archipelago (20° 30'S, 116° 42'E). Mats consisted mainly of the non-heterocystous, filamentous genera Microcoleus, Phormidium, Oscillatoria and the coccoid genus Aphanocapsa. Nutrient status, chlorophyll levels and organic carbon contents were determined and, in addition, nitrogen fixation and nutrient export by tidal water were measured. Three main factors appeared to affect algal mat distribution on tidal flats: tidal height, degree of tidal current and sediment influx, and conditions of drainage.

These algal mats bind and stabilize substrate to prevent severe erosion and conserve moisture. They are rich in organic matter and serve as a store for carbon (500-800 g m^{-2}), nitrogen (14-21 g m^{-2}) and phosphorus (0.7-1.5 g m^{-2}). These levels are similar to other algal mat systems. High levels of chlorophyll production (7.4 mg chl *a* m^{-2} d^{-1}) and acetylene reduction (1100-1300 um C_2H_4 produced m^{-2} hr^{-1}) were recorded at salinities between 20 °/oo and 60 °/oo in the laboratory. *In situ* studies at one site showed low rates of nitrogen fixation (8-60 um C_2H_4 produced m^{-2} hr^{-1}).

Loss of nutrients may occur when desiccated mat portions are carried by wind, and by leaching. Laboratory experiments showed considerable loss of nitrate from mat sections exposed to freshwater, indicating that rainfall may be significant in contributing to nutrient loss. Data indicate that significant particulate organic nitrogen and phosphorus, derived from dead organic material, could be transported out of a system by the tide. These nutrient losses, which may be up to one-half of the nitrogen contained in the biomass, were considered to be a significant source to mangroves.

CONTENTS

FIGURES

Page

Page

TABLES

Page

APPENDIX

Figures

Tables

1. INTRODUCTION

There has been much speculation about the importance of mangroves to coastal ecosystems (Lugo and Snedaker, 1974), and particularly the role of mangroves in supplying tidally-exported detritus to coastal waters (Boto and Bunt, 1981). These authors consider decomposition within the mangrove system to be insufficient to replenish the losses of nutrients in this detritus; this must be replaced by some external source. Along tropical, humid coastlines the inland vegetation is likely to provide this source, but it is thought that in dry areas the ocean supplies nutrients.

Fosberg (1961) was first to draw attention to the occurrence of "vegetation-free" zones on dry mangrove coasts. He observed this phenomenon in Queensland (Australia), Ecuador, Salvador and the Honduras where the coastlines have two factors in common; a very large tidal range and a dry, or seasonally dry, climate (less than 1000 mm of rain per year). The bare zone, which is intertidal, was thought to result from an interaction between inundation and extreme dryness, causing salt concentrations which exceed the tolerance of both mangroves and halophytic shrubs.

The tropical, arid coastline of the Pilbara which has a low, erratic rainfall (277 mm per year) and a five metre tide range (Kenneally, 1982; Chittleborough, 1983) also possesses bare zones behind mangroves along most of its coast. On closer examination, however, many of these intertidal flats were found to be covered with well developed, blue-green algal mats. Algal mats occur behind and within mangroves of other systems; for example in West Africa (Aleem, 1980) and the Sinai Peninsula (Potts and Whitton, 1977; Potts, 1979, 1980).

An algal mat is a cohesive fabric consisting of a community of cyanophyte filaments, usually incorporated within an organic sediment (Golubic, 1973). Mats may be dominated by a single species (Jones, 1977a) or may be communities of a number of different cyanophytes (Sanders, 1979). Nitrogen fixation by the heterocystous and non-heterocystous genera of blue-green algae that form algal mats is known to occur in some mangrove systems (Potts, 1979). In addition, green and red algae, animals, fungi and abundant bacteria are often part of an algal mat community (Bauld, 1981b; Tison et al., 1981).

Mangroves cover 70 km^2 of the Dampier Archipelago, and therefore form a prominent part of the coastal ecosystem (Gordon, 1983). The major objective of the work reported here was to determine the role of blue-green algal mats in the mangrove ecosystem. The approach taken was to observe the spatial and structural variation in algal mats within and between study sites, and to describe the factors affecting growth and decay. Investigations were made as to whether nitrogen is fixed in sufficient quantities for fixation to be a significant source of nitrogen to mangroves via leaching from algal mats.

2. THE STUDY AREA

2.1 GEOLOGY AND CLIMATE

The coastline near the Dampier Archipelago (Figure 2.1) borders a hinterland with an arid climate. Geologically this area is a flat depositional plain 12-15 km wide in the south, decreasing to 2-3 km in the north-east; sandy and silty near major rivers and fine textured elsewhere. Peninsulas and islands serve to shelter most of the coast from onshore waves (Galloway, 1982).

Much of the Dampier coast is Pre-Cambrian (Semenuik et al., 1982). Pleistocene limestone occurs locally on the Pre-Cambrian rock and overlying all rock types is a layer of sand and gravel or mud deposits of marine origin, the thickness of which depends upon elevation and exposure to waves and currents. The Dampier 'Peninsula' is in fact an island that was once separated from the mainland at high tide. The building of a causeway in 1969 and the use of part of the coastal salt flats as solar production ponds since 1972, has connected it to the mainland (Figure 2.1).

The climate of the Dampier region is both tropical and arid. January to June are the hottest six months of the year. Evaporation is greater, by an order of magnitude, than the rainfall, which is low and erratic (270 mm per year, Figure 2.2a) (Chittleborough, 1983). The year of this study, 1983, was considerably drier than average (Figure 2.2b). Rainfall is associated with cyclonic activity; the cyclone season being from December to April. On average, a cyclone passes within 100 km of the coast every two to three years (Semenuik et al., 1982).

Air temperatures range from 12-45 ^{o}C and water from 17-35 ^{o}C, although water ponded on algal mats has been measured at 60 ^{o}C, and that trapped in tidal creeks at 80 ^{o}C.

2.2 STUDY SITES

Methods

Blue-green algal mats occur extensively on the coastal salt flats behind mangroves on the Dampier Archipelago and at other areas of the Pilbara coast (Exmouth to Port Hedland). Four sites were chosen for this study (Figure 2.1); a major consideration in selecting sites was accessibility to the Dampier field station of the Department of Conservation and Environment. The following sites were chosen:

King Bay South. A discrete embayment which was fed by a seasonal creek at the south-west (Figure 2.3); 0.51 hectares of blue-green algal mat were patchily distributed on this tidal flat.

Dampier Salt. This area consisted of approximately 30 hectares of algal mat on a mudflat which had been truncated by a levee constructed by Dampier Salt Pty Ltd. This restricted flushing landward of the algal mat (Figure 2.4).

Nickol River. A remote area that had restricted access by road and was inaccessible by vehicle after high spring tides, owing to the flooding of the salt flat area (Figure 2.5). There were 65.9 hectares of patchily distributed mat in this area.

Karratha. This area was the most eastern part of an extensive, 170 hectare algal mat located 1 km from the nearest mangroves (Figure 2.1). This algal mat probably extended over 740 hectares before being recently covered by silt from two rivers, one of which drains the townsite of Karratha.

Assessment of algal mat cover at each study site was calculated from aerial photographs of the Dampier coastline by planimetry using an electronic digitizer (Summagraphics Corp., Fairfield, Connecticut, USA). The extent of tidal erosion in the Dampier Salt locality (Figure 2.1, 2.6) was determined

by digitization of the algal mat area from aerial photographs taken in 1980 and 1981.

Tidal velocities in King Bay were determined by timing the passage of drogues over a specified distance within tidal creeks on flood and ebb tides.

2.3 VEGETATION

There are seven species of mangroves on the Pilbara coast. This coast is the southernmost zone along West Australian shores where assemblages of more than one species of mangrove occur. As one moves north-east along this coast, the coastal plain deepens and the mangrove zone narrows. A very narrow belt of mangroves fringes rocky shores in the Dampier Archipelago (Kenneally, 1982). These do not penetrate up the main rivers, which are tidal for very short distances and dry for most of the year, but they fringe short tidal creeks that dissect parts of the coastal plain.

The present study found blue-green algal mat growing on the salt flats behind the most landward mangroves, Avicennia marina. The distance between algal mat and mangal varied from 1 km at Karratha to four metres at King Bay (Figure 2.3). Occasionally blue-green algal growth occurred on pneumatophores within mangrove stands. The only other vegetation on the salt flats consisted of two halophytes, Wilsonia backhousii and Arthrocnemum sp., which grew on higher elevations within and behind the mudflats. Algal mat, at its most seaward edge, grew amongst these halophytes only at Nickol River and Dampier Salt, and when it did so, the mat growth form was extremely patchy.

No other vegetation, besides the halophytes, occurred on the hypersaline areas landward of the algal mat.

2.4 FAUNA

The main inhabitants of the mudflats were fiddler crabs, Uca sp., Metapograpsis sp. and Sesarma sp.; these were active at low tide and foraged on exposed mud surrounding algal mats, although they were never observed to feed on the mat itself. Much damage was done to the seaward edge of the algal mat by a hermit crab that inhabited only cast-off shells of the mangrove snail, Telebralia palustris. This crab was observed to feed on the mat when it was exposed by the receding tide. At high tide, particularly in King Bay, sea mullet schools fed on algal mat edges.

Disturbance of algal mats on a large scale appeared to result from human activity. The regular use of mud flats by the public for trail bike riding and as access to the mangroves for fishing, caused considerable damage to the mats. There was both immediate, local destruction and long term alteration of tidal flow, which eroded the mat. These effects were particularly prevalent in areas such as King Bay and Karratha, that were easily accessible to the public. Areas with restricted public access (Dampier Salt) or those that were remote (Nickol River) suffered much less damage.

2.5 TIDES

The algal mat at King Bay was inundated on 245 days of the year (Chapter 5), and was underwater for approximately 4-6 hours on each of these days. The longest period of continuous exposure, between bimonthly tidal cycles, was seven days. Nickol River and Karratha were likely to have had similar regimes. In summer, the algal mat in these areas dried rapidly after a

spring tide but in winter the mat stayed moist for longer periods; the soil under an algal mat stayed moist at all times of the year.

The mat at Dampier Salt was different from these areas in two main respects. Firstly, the levee behind the algal mat restricted tidal flushing (Figure 2.1), and secondly there was a ponding effect where tidal outflow was restricted, after a high tide, by a sill of sediment at the seaward edge. This ponding caused water to remain over the algal mat area until it evaporated, a process that took one day in summer and several days in winter.

Large scale loss of mat was occurring at the Dampier Salt site because of tidal-creek headwater erosion. This erosion caused dehydration of the higher tidal flat surface and the concommitant loss of algal mat in areas close to tidal creeks. In the period from 1980 to 1981, the algal mat area at Dampier Salt decreased from 42 hectares to 31.9 hectares owing to the cutback by tidal creeks (Figure 2.6).

At King Bay, similar erosion was occurring on a smaller scale where tidal-creek course-changes degraded the mat edge. Tidal scour occurred here, particularly on high spring tides when the current velocity in creeks could reach 500 mm s^{-1}, removing both sediment and mat in bordering areas.

Tidal erosion and scouring were less prevalent at Karratha and Nickol River because of slower tidal current velocities in these areas.

2.6 SUMMARY

- The extremely arid climate of the Dampier coastline results in an unusual feature of its mangrove swamps; that of extensive salt flats to their landward side.
- The only vegetation present on these flats were blue-green algal mats and the halophytic shrubs, Wilsonia backhousii and Arthrocnemum sp.
- The main faunal inhabitants of the algal mat were crustaceans. One species, a hermit crab inhabiting Terebralia palustris shells, grazed on the mat.
- Large scale destruction of the algal mat was caused by recreational activities.
- Four areas were selected for intensive study : King Bay, Nickol River and Karratha as sites frequently flushed by the tide, and Dampier Salt where water remained for extensive periods. Initial observations indicated that tidal-creek headwater erosion and scour may have caused losses of algal mat at King Bay and Dampier Salt.

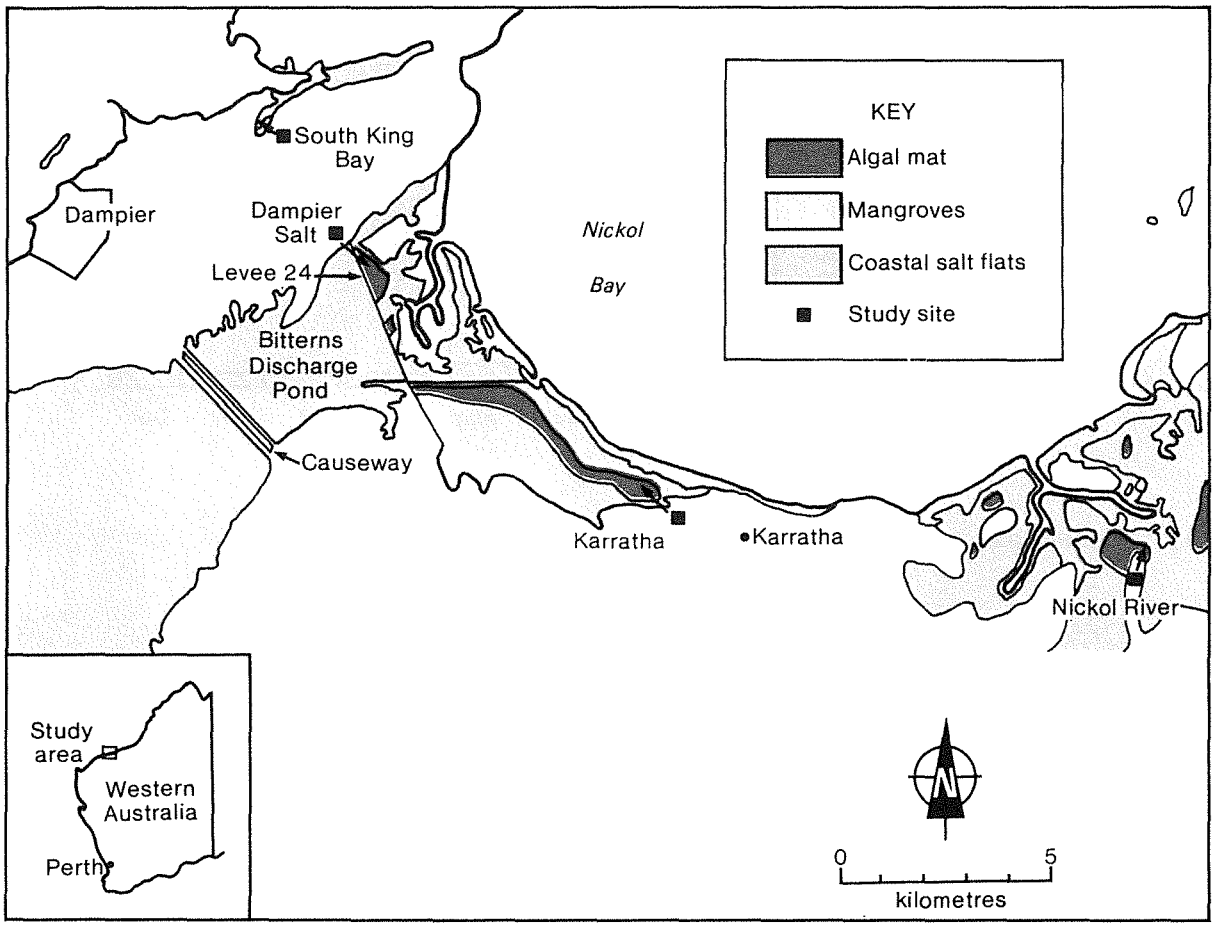


Figure 2.1 The study area showing distribution of algal mats, mangroves and salt flats, and position of study sites. Insert shows location of study area in Western Australia.

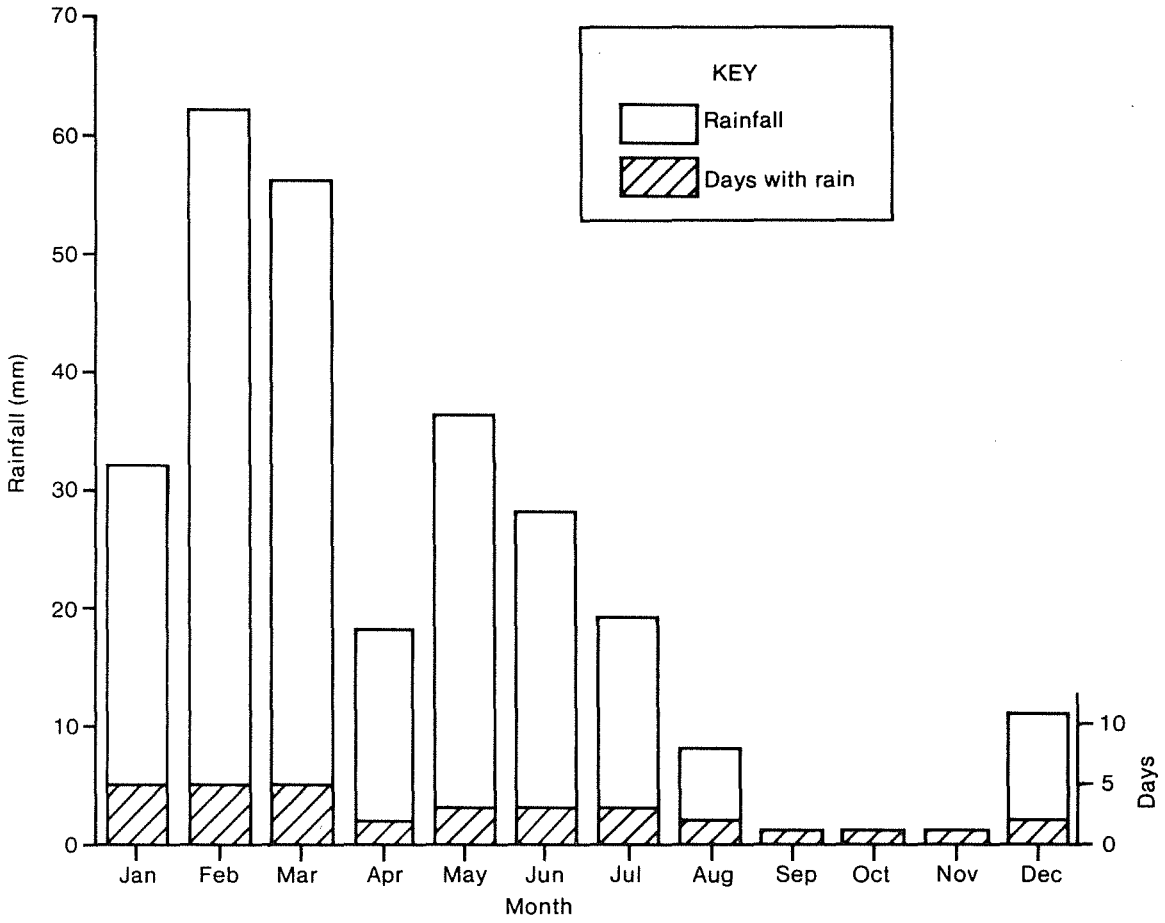


Figure 2.2a Average monthly rainfall at Dampier (1969-1982)

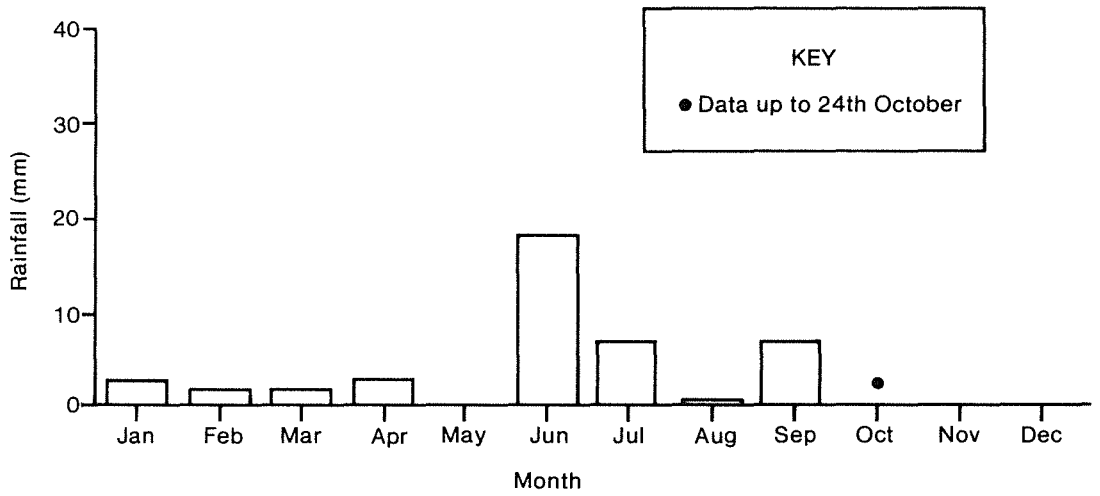


Figure 2.2b Monthly rainfall at Dampier (1983)

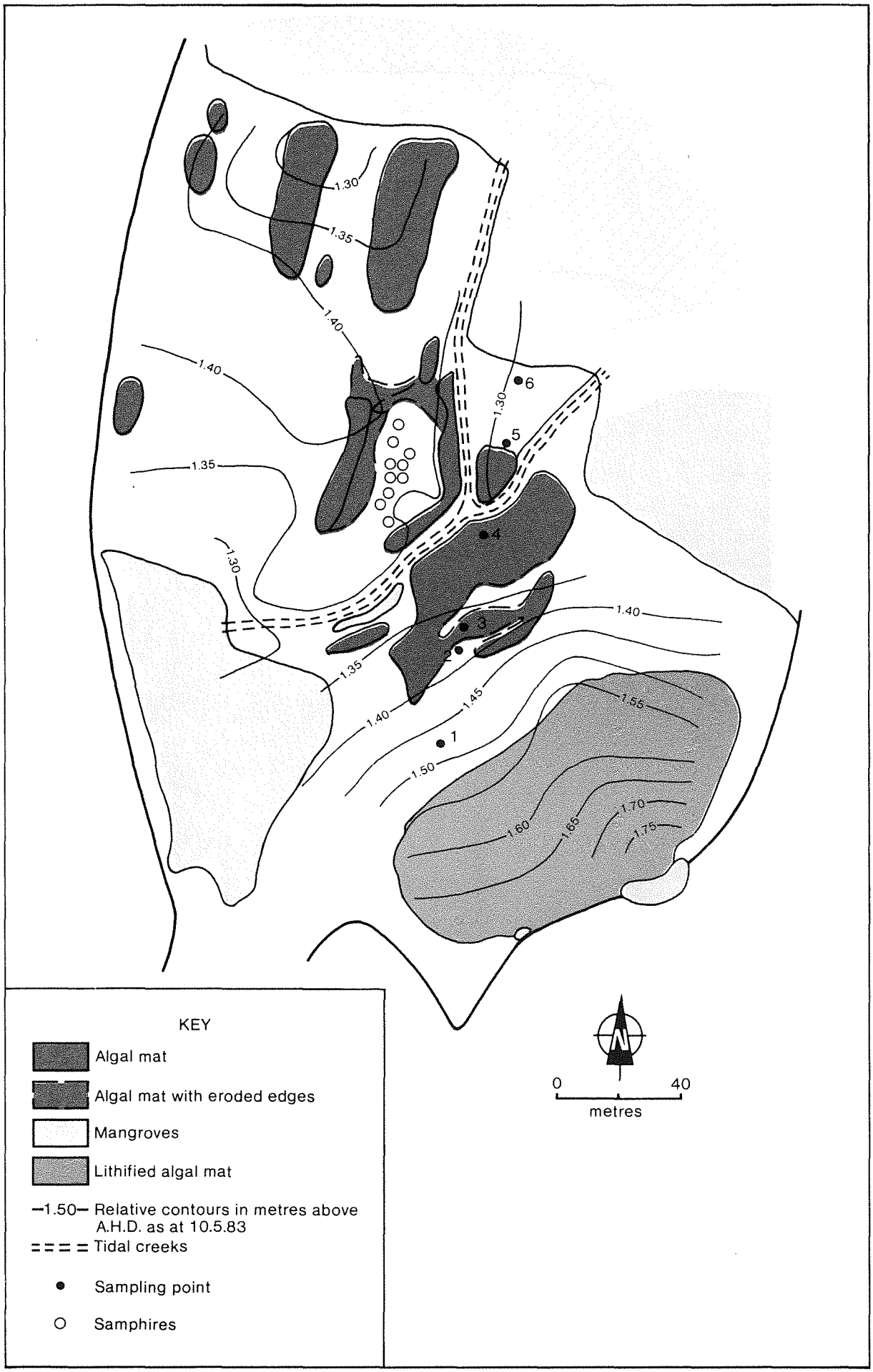


Figure 2.3 King Bay study site.

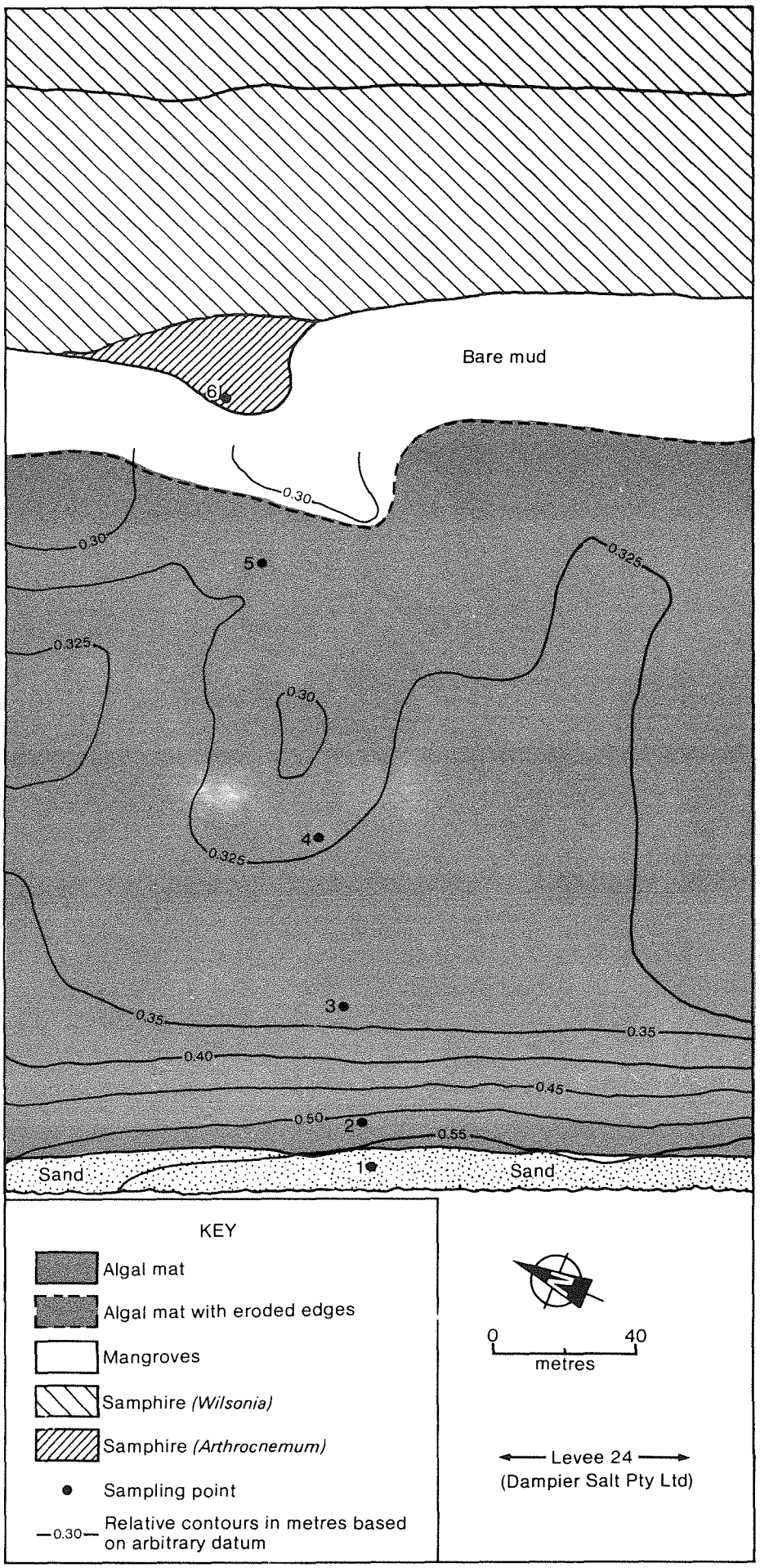


Figure 2.4 Dampier Salt study site.

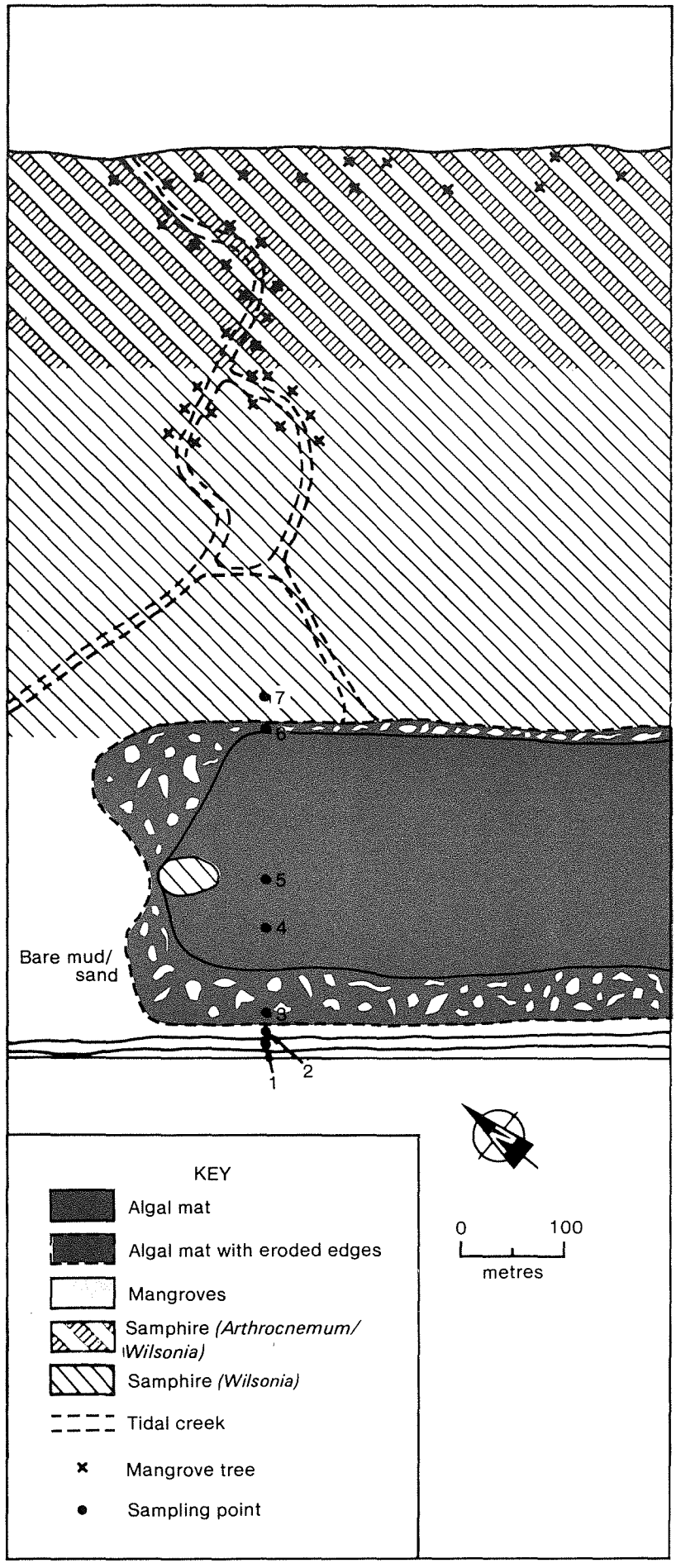


Figure 2.5 Nickol River study site.

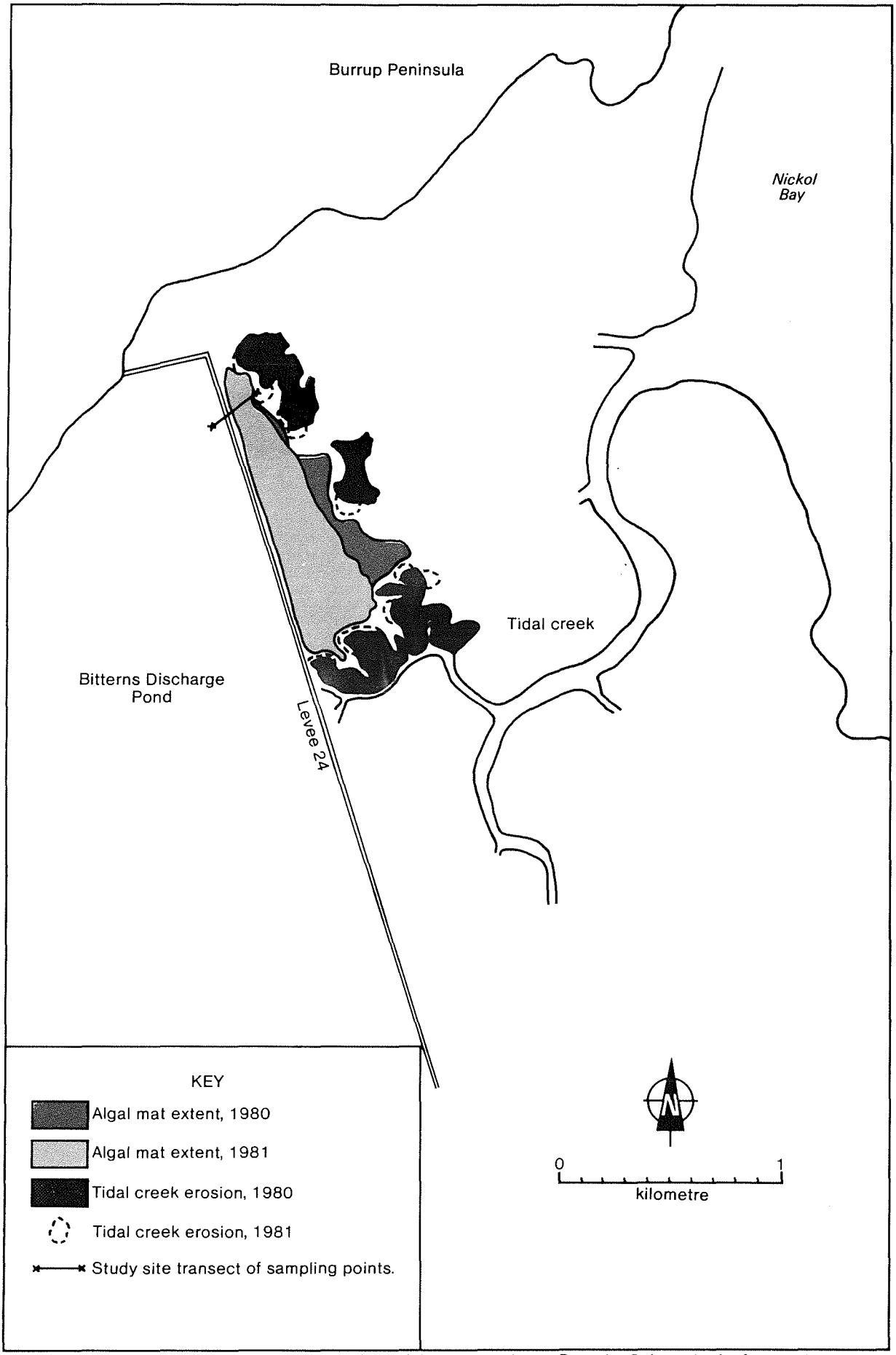


Figure 2.6 Reduction in algal mat area caused by tidal creek erosion at Dampier Salt study site from 1980 to 1981.

3. THE STRUCTURE AND TAXONOMY OF DAMPIER ALGAL MATS

3.1 INTRODUCTION

Fewer taxonomic studies have been made of marine blue-green algae than of freshwater species and, as a result, the marine forms are relatively poorly described (Potts, 1980). The requirement of high-powered light microscopy to identify species of Cyanophyta, the considerable range of environments in which they occur and structural variation renders classification of genera and species difficult. Drouet (in Humm and Wicks, 1980) considered that much of the previously measured variation was environmental, and reduced the number of species. In his classification there are no distinct orders and only eight families, but this rather drastic reduction has not been generally accepted (Potts, 1980). A rationalization of the nomenclature of the many genera and species will be advantageous in further ecological studies.

Certain heterocystous and non-heterocystous cyanobacteria in algal mats appear to have a cosmopolitan distribution, although they often occur in different associations (Bauld, 1981b). The main mat-producing genera are divided into two types, the coccoid forms (eg. Aphanocapsa, Gleocapsa and Aphanothece) and the filamentous forms (eg. Oscillatoria, Lyngbya, Microcoleus, Phormidium and Nostoc).

An algal mat is a complex entity (Figure 3.1) consisting of cyanobacteria, green algae and abundant bacteria. It may be dominated by a single species of blue-green algae or by a number of them. The purpose of this study was to consider the algal mat as a unit in relation to its ecological significance, especially as a nutrient source. A brief taxonomic and structural investigation, however, was undertaken to provide background information for understanding ecological function. Taxonomic work was

limited to identification of genera rather than species, with only one exception.

3.2 METHODS

Samples of algal mat were collected in March, April and July, 1983 from King Bay, Dampier Salt and Nickol River. These were examined immediately. Samples were also examined from glasshouse cultures of Nickol River and King Bay algal mats grown at salinities varying from 0 to 140 ^{o}/oo (Chapter 4). For taxonomic purposes, mats were teased apart with dissecting needles, mounted in seawater (36.4 ^{o}/oo) and examined by light microscopy. Classification of genera was carried out using keys from Desikachary (1959) and Drouet (in Humm and Wicks, 1980). Structural variation was determined by the collection and measurement of macroscopic stratification in 19 mm diameter algal mat cores taken at five to 20 m intervals along the transects at each site, except Karratha, in March, April and July 1983 (Figures 2.3, 2.4 and 2.5).

Gas bubbles that had evolved on immersed mat surfaces in glasshouse-grown samples were collected and analysed on a Shimadzu GC-6AM Series Gas Chromatograph, using a thermal conductivity detector (TCD-6) and incorporating a 3.5 mm O.D. x 2.0 mm I.D. x 1 m column packed with 100-120 mesh Porapak T. The column was run at 130 ^{o}C with argon, the carrier gas, flowing at 35 ml min^{-1}. Air was used as a standard for nitrogen and oxygen levels.

Samples of soil were collected from beneath the algal mat at each site, stored in sealed plastic bags and freighted to the University of Western Australia. Soil textures were determined, after air drying for one week, by

the separation of 50 g of soil in a solution of sodium hexametaphosphate ('Calgon': 125 ml of 40 g L^{-1} solution in 875 ml of deionized water). A Boyoucos hydrometer was used to measure the proportions of silt and clay (after 40s of mixing) and clay (after 120 min).

3.3 RESULTS

Major species and composition of algal mats

All cyanobacterial species in the algal mats examined were non-heterocystous.

King Bay algal mats were dominated by Microcoleus chthonoplastes Thuret (M. Borowitska pers. comm.), which made up 80-90% of the total species present. Oscillatoria constituted 5-10% of the genera and Phormidium made up a small proportion. Other phyla included a unicellular chlorophyte and a pennate diatom. In general these mats had a high proportion of sand particles bound within the cyanobacterial filaments (trichomes).

Algal mats from Nickol River had very low quantities of sand and sediment and consisted mainly of fine organic particles. The major cyanobacterial genera were Phormidium (50% total), a unicellular Chroococcaceae, possibly Aphanocapsa (40%) and a proportion of Microcoleus. Other phyla were scarce.

At Dampier Salt two forms of mat were present, and these were arbitrarily classified by their appearance into 'wet' (a thin, light-green form) and 'dry' (a thick form with a white surface). 'Wet' mats consisted exclusively of Phormidium, with little incorporated sediment or fine particulate matter. The 'dry' mat contained Phormidium and possibly Lyngbya but in much smaller quantities than in 'wet' mats. Most of this mat consisted of particulate matter with a crust of unidentifiable material on the surface.

The lower brown/black laminations of mats from each site were composed mainly of dead or empty trichomes and fine particles.

Nickol River and King Bay mats were similar in cyanobacterial composition at or above a salinity of 40 $^{o}/_{oo}$. There was less growth of all genera at salinities of 100 $^{o}/_{oo}$ or higher. New growth of Nickol River mat, as a light green film, in freshwater (0 $^{o}/_{oo}$) was exclusively of the Chroococcoid genus, Aphanocapsa, which was not present at 20 $^{o}/_{oo}$. The major form at this salinity was Phormidium. With King Bay mat immersed in freshwater, large numbers of Phormidium filaments were found combining into a thallus; at 20 $^{o}/_{oo}$ this thallus also contained groups of Microcoleus.

Seasonal and spatial variation

Each site had a similar soil texture, a 'loamy sand' consisting of 77-79% sand, 7-13% clay and 10-14% silt. The presence of more water at Nickol River and Dampier Salt caused this soil to become a mud. King Bay soil, however, which was better drained, was more compact.

The amount and type of laminations varied between and at sites (Figure 3.2, 3.3). King Bay had similar laminations along the transect (a cyanobacterial layer of 0.5 mm to 1 mm thick, and a brown laminated layer of 5 mm to 7 mm), while at Dampier Salt there were no laminations under 'wet' mat, and up to 10 mm under 'dry' mat. Nickol River had a similar appearance to mats examined at Dampier Salt.

There was little change in structure of the mat at King Bay from one sampling date to the next, but mats at the other two areas became more 'tufted' when rapid growth occurred in May and July.

The bubbles from the algal mat surface contained slightly more oxygen than air (27-28%, compared with 21% in air) and less nitrogen (72-73%).

3.4 DISCUSSION

The occurrence of only non-heterocystic cyanobacteria in the Dampier algal mats is surprising as heterocystic genera are known to be present in this area (Sammy, 1979). While the highest rates of nitrogen fixation are usually found in mats containing only or predominantly heterocystous genera (Warmling, 1973; Potts and Whitton, 1977; Wickstrom, 1980; Reynaud and Roger, 1981), high rates have also been found in mats containing only non-heterocystous forms (Bohlool and Wiebe, 1978; Wickstrom, 1980). These non-heterocystous mats have also been found in tropical intertidal zones (Potts and Whitton, 1977), temperate estuaries (Leschenault Inlet, Western Australia, Paling unpub. obs.) and Antarctic lake bottoms (Allnut et al., 1981; Love et al., 1982).

Only one study has suggested that heterocystous and non-heterocystous cyanobacteria may be differentially distributed in mats in the same area. In the Gulf of Elat (Aquaba) (Potts, 1980) heterocystous cyanobacterial genera, in mangrove environments, were restricted to intertidal zones and pneumatophores. No heterocystous genera occurred in coastal pools or on mangrove sediments; these were dominated by non-heterocystous forms. Potts (1980) suggested that the greater availability of nutrients in the pools and sediment allowed the development of non-heterocystous flora. This has not yet been substantiated, but it remains the only theory proposed so far to explain the distribution of heterocystous and non-heterocystous genera in any habitat.

Visible gas evolution from algal mats has been documented elsewhere only once (Parker et al., 1982). In this case, the non-turbulent environment under the ice in Antarctic lakes allows large oxygen bubbles to evolve and lift the mat off the substrate, floating it to the surface. This also causes lake waters to become super-saturated with oxygen. In glasshouse-grown algal mats the oxygen content of these bubbles would be reduced, as observed. This is likely to occur because the relatively slow rate at which bubbles form allows ample time for equilibration with the dissolved gases in the water. At Nickol River and Point Sampson (Paling, unpub. obs.) bubbles have been observed on algal mats in situ within one hour of tidal inundation. The rapidity of this reponse suggests that, when the mats were inundated, photosynthetic activity was very high.

The low number of species present in the Dampier algal mats and the occurrence of mostly cyanobacterial genera rather than other phyla (particularly in the monospecific Dampier Salt 'wet' mat) indicate that this area was under some type of stress. Sanders (1979) found that species diversity in algal mats in situ decreased with increasing salinity. The survival of mat species from Dampier at artificially high salinities show that they were at least halotolerant. This was not the case in experiments conducted by Sanders (1979), where a salinity of 20 $^{o}/_{oo}$ was sufficient to reduce the number of dominant species to one.

High temperatures in the Dampier Archipelago reduce water availability and increase evaporation rates. These combine to produce high salinities. Wickstrom (1980) found that high temperatures along a thermogradient were sufficient to reduce the number of cyanobacterial species from seven to three in algal mats growing in thermal springs. In a fluctuating thermal regime, Tison and others (1981) found that cyanobacterial species dominated

areas with temperatures above 45oC. When temperatures dropped for long periods below 40 °C in the same area, species from other phyla began colonization. The algal mats in these areas, unlike those of the Dampier region, were not stressed by high salinity. The presence of more numerous dominant species in Nickol River algal mats may indicate that environmental stresses were generally less extreme in this habitat. Water availability, for example, was greater at this site than at others as indicated by the moisture content of the soil.

Increased mat growth, indicated by surface lifting at Dampier Salt and Nickol River in May and July, reflected a reduction in environmental stress; temperatures were lower, more water was available (Chapter 2) and salinity was not as high. King Bay algal mats, on the other hand, changed little in these periods suggesting less favourable conditions there.

Further intensive field monitoring is necessary to clearly define the relative influence of salinity, temperature and desiccation on algal mat growth and composition in the Dampier region.

3.5 SUMMARY

- Non-heterocystic blue-green algal genera dominated the algal mats at all sites studied in the Dampier Archipelago.
- King Bay mats were dominated by the genus Microcoleus, Nickol River by a Phormidium - Aphanacapsa association and Dampier Salt by Phormidium.
- The dominance of the algal mats by cyanobacterial species indicate that these areas were probably stressed by a combination of high temperatures, reduced water availability and high salinities.

- Visible gas evolution in inundated mats suggests that they had a high rate of photosynthetic activity when immersed; this has been documented for algal mats in other areas only once.
- Each site had similar soil textures but different structures associated with varying water content. Nickol River and Dampier Salt soils contained more water than King Bay.
- King Bay algal mats varied less in growth rate, species composition and laminations during the period sampled. Better drainage and hence lower water availability, compared with the other sites, may have been the cause of these characteristics.

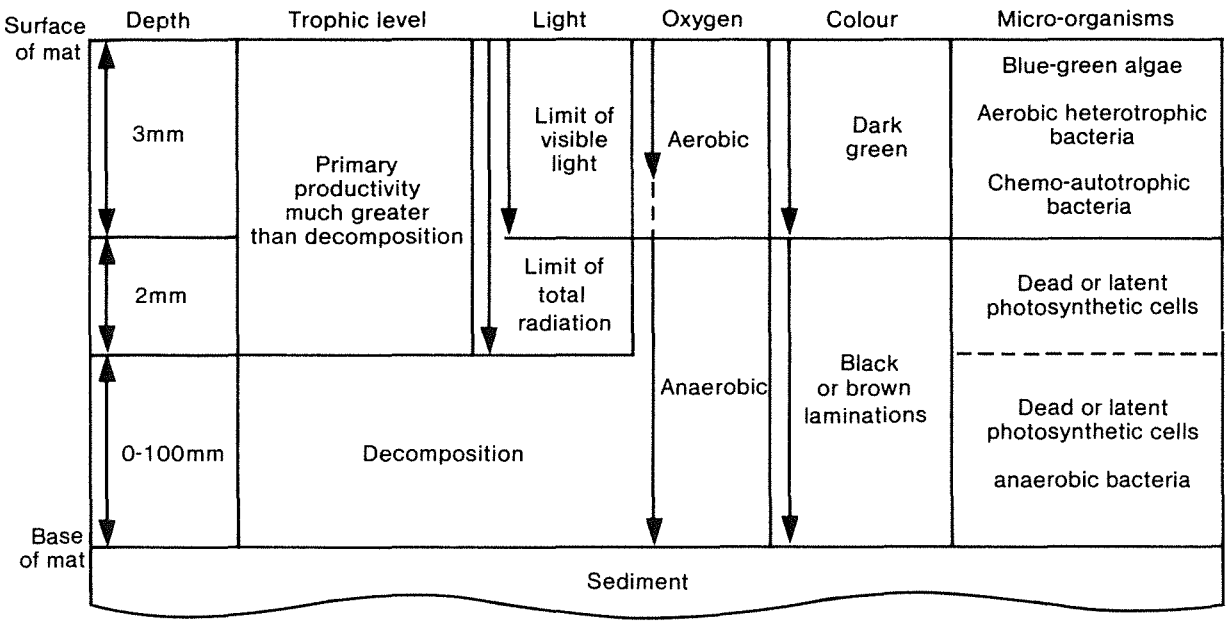


Figure 3.1 Diagrammatic representation of an algal-bacterial mat (modified from Javor *et al.*, 1979)

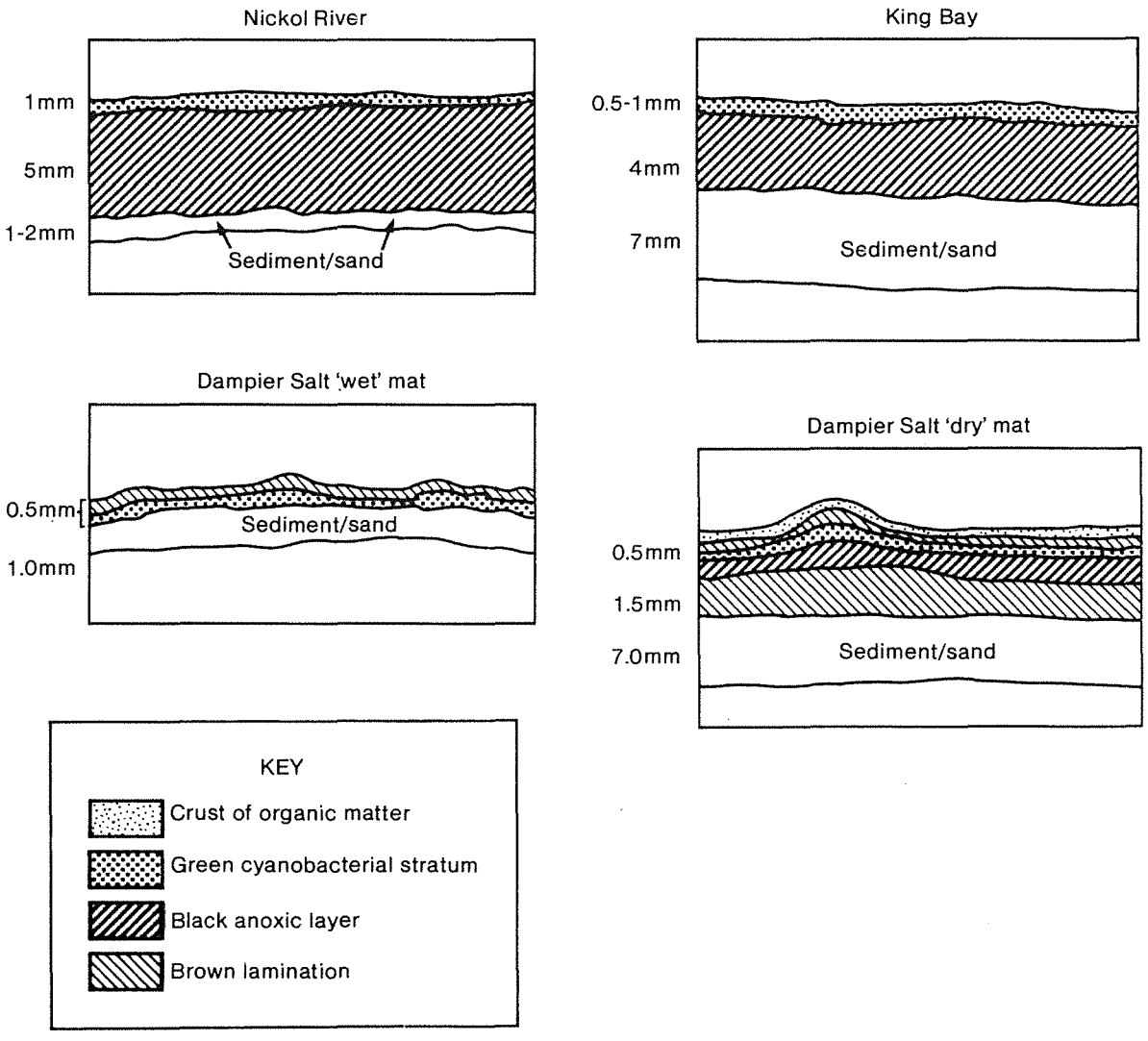


Figure 3.2 Stratification of algal mats at each study site.

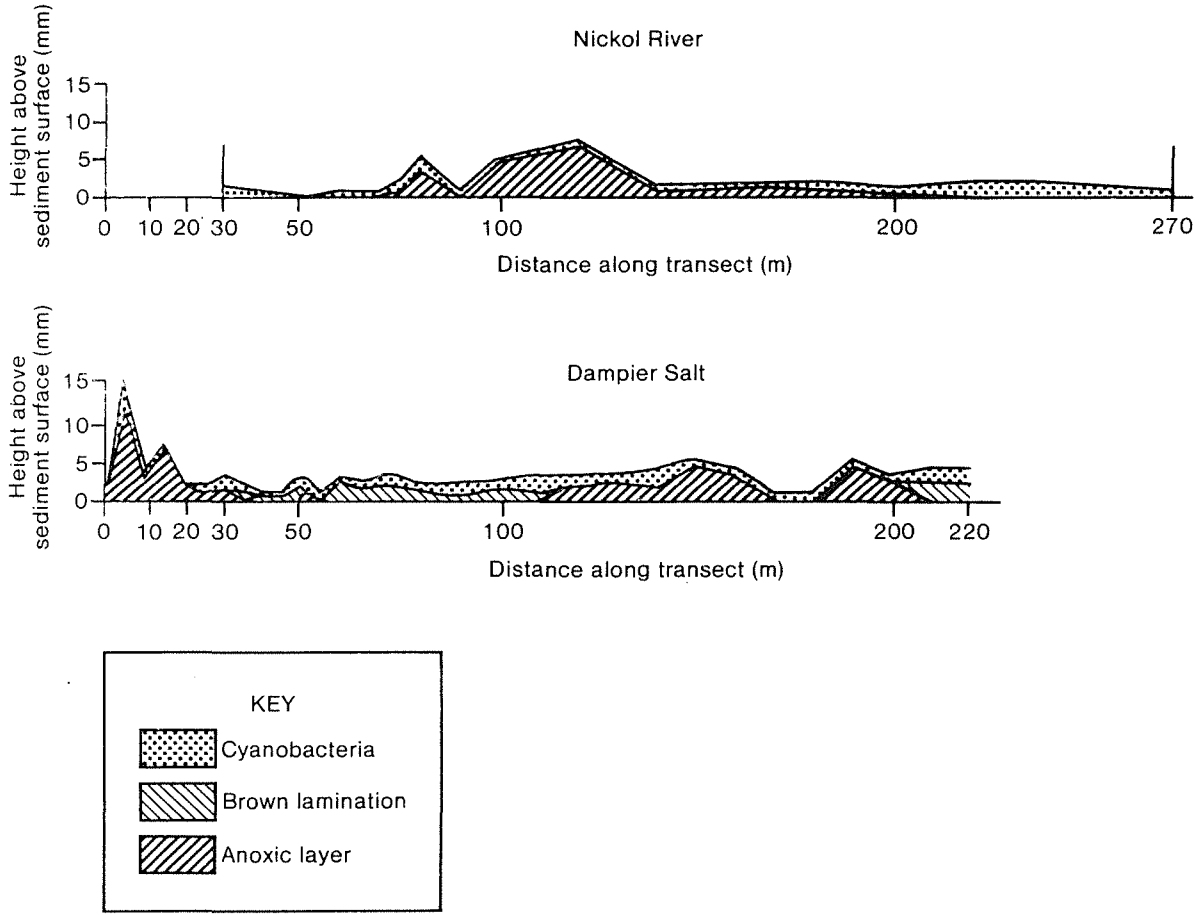


Figure 3.3 Cross sections of strata in algal mats along transects at Dampier Salt and Nickol River.

4. THE EFFECT OF ENVIRONMENTAL FACTORS ON ALGAL MAT GROWTH

4.1 INTRODUCTION

Cyanobacteria occur in a wide range of terrestrial and aquatic environments (Fosberg, 1961; Golubic, 1973), but are limited in their distribution to areas that are more or less extreme. Algal mats occur in environments ranging from lakes in the Antarctic (Parker and Simmons, 1981; Parker et al., 1982) and Arctic (Gersper et al., 1980), to highly saline lakes (Bauld, 1981b) and hot springs (Doemel and Brock, 1977). Evidence for algal mats in deep ocean, thermal vents has also been documented (Jannasch and Wirsen, 1981).

There is geological evidence, from the presence of microfossils and stromatolites (Awramik et al., 1980), to suggest that mats and similar structures were more widespread throughout the Pre-Cambrian, but declined thereafter (Bauld, 1981b). The scattered, present-day distribution of algal mats may result from their tolerance of factors that effectively remove competition and grazing, such as salinity (Erdmann, 1983), heat and solar radiation. Bauld (1981a) has suggested that, in the absence of grazing, microbial mats would be more common than they are at present, and theorised that the reduction in distribution of Pre-Cambrian mats was caused by the advent of grazing, and burrowing, animals. If this is the case, cyanobacterial mat-building genera have had ample time to adapt to the fluctuating salinities and marginal inundation that exists in their present-day niche.

Information on cyanobacterial mats in general remained dispersed until they were well-reviewed by Bauld (1981a, 1981b). There is evidence that mats play an important role in salt lake ecosystems and the preservation of organic carbon. They may be major contributors to primary productivity although little work has been carried out on this aspect.

Physical parameters which are thought to be of main importance for algal mat growth are temperature (Jones, 1977e; Ward, 1978), hydrologic regime (Fosberg, 1961), salinity (Sanders, 1979) and water availability (Golubic, 1973; Sammy, 1983). In the Dampier region, the arid coastline and low rainfall provide conditions in which algal mats can grow. A number of environmental parameters were measured in relation to mat distribution during two field trips. These field observations were supplemented by experimental growth trials to determine the factors that significantly affect algal mat growth in this region. In addition, information was sought concerning the nutrient content of mats, groundwater and mangrove leaf litter as background information for subsequent work on nutrient cycling. Details of methods of collection and analysis are given in Paling (1983).

4.2 METHODS

Groundwater Measurement

Salinity and metal cations. Samples for groundwater (subsurface) salinity and cation determination were obtained by excavating the soils to reach free water at points along a transect of each study site (Figures 2.3 to 2.5). Salinities were measured using a portable, temperature-compensated refractometer (American Optical Company, U.S.A.) calibrated with standard seawater. Salinities were measured in this way at all sites in early March and twice in late April 1983 at King Bay and Dampier Salt. Groundwater salinities were measured after tidal cycles by taking samples before and after high tides in King Bay and areas in which tidal water remained around the algal mat at Nickol River.

Groundwater samples were collected in March along the transect at Dampier Salt for metal cation analysis, as it was thought that the adjacent bitterns

pond behind the algal mat (Figure 2.1) may have contributed to the high salinities recorded. Samples were analysed for Na, Mg, Ca and K using an Atomic Absorption Spectrophotometer following the methods described in Atkins et al. (1978). Chloride concentrations were analysed using a solid state chloride electrode attached to a pH meter (Orion Research). The cation analyses were compared to seawater concentrations (Bayly and Williams, 1973) and the Mg/K ratios of bitterns discharge water - the residual 'brine' solution following extraction of salt from the evaporated ponds of the salt works (Bitterns Discharge Program, 1981).

Nutrients. Groundwater samples were collected at the same points as those for salinity measurement. They were placed in one litre plastic bottles and kept cool in the field. The mud fraction was allowed to settle in the cold, and samples for total nitrogen (TN) and total phosphorus (TP) decanted into Whirl Paks and frozen. Water for nitrate (NO_3-N), phosphate (PO_4-P) and ammonium (NH_4-N) analysis was filtered under vacuum through Whatman GFC filters, poured into Whirl Paks and frozen.

One groundwater sample was collected at each transect from all study sites in March. In April, three replicates were collected at each transect and one metre either side at King Bay and Dampier Salt.

Nutrient analyses were carried out at the Botany Department, University of Western Australia. Total nitrogen, nitrate, ammonium nitrogen, total phosphorus and orthophosphate were all analysed after the methods of Atkins et al. (1978).

Algal mat dry weight, organic carbon content and surface temperature

Sample collection. In March, a number of 19 mm diameter cores of algal mat were collected from each sampling point on the transects at King Bay, Nickol River and Dampier Salt with a standard coring device. Ten cores each of 'wet' and 'dry' mat from Dampier Salt (Chapter 3) were collected to compare the two forms of mat. Two short transects of 5 m and 7 m long, and at right angles, were made from sampling point 4 at King Bay to the adjacent tidal creeks (Figure 2.3). Squares of mat (50 x 50 mm) were removed every 0.5 m along each transect.

Algal mat that had dried and broken free after erosion ('friable' mat) was collected at Dampier Salt and King Bay for analysis. Representative samples for organic carbon analysis were collected from each study site. Temperatures on the mat were measured along each transect using a standard thermometer, the bowl of which was wrapped in foil to minimize solar absorption. Measurements were also made at a depth of 20 mm into the mat.

In April a more complete procedure was used; ten cores of algal mat were collected in a 1 x 1 m square at each sampling point and 1 and 2 m either side of each sampling point at King Bay and Dampier Salt for wet weight, dry weight and carbon analysis. Nickol River was not sampled owing to its inaccessibility by vehicle after spring tides.

Sample analysis. Algal cores were trimmed of excess sediment in the field laboratory, weighed, oven dried overnight at 110 ^{o}C and reweighed after cooling in a desiccator. Samples were freighted to the Botany Department, University of Western Australia, where organic carbon was determined by the loss-on-ignition method. Details of methods are given in Paling (1983).

Results are presented as % organic carbon (of dry weight) or in g m-2 obtained after multiplying the algal mat core area by the appropriate factor. This factor was determined by measuring the dry weight of algal mat samples of different areas. All organic carbon figures, unless otherwise stated, are the products of ten replicates. Statistical analysis consisted of two-tailed t-tests and ANOVA tests between means and groups of means from each sampling point (Zar, 1974). Most statistical results were derived using the statistical package program (S.T.P.) maintained by the W.A. Regional Computing Centre at the University of Western Australia.

Algal mat chlorophyll content

Five 19 mm diameter algal cores were collected in March and April from each of the sampling points along the major transects described above. These were trimmed of excess sediment, placed into 10 ml plastic centrifuge tubes and frozen in the dark. At the University of Western Australia, these were extracted in acetone and the content of chlorophyll *a*, *b* and $c_1 + c_2$ read on a Varian DMS 90 UV Visible Spectrophotometer. Details of sample treatment and analyses are given in Paling (1983).

Concentrations of chlorophyll *a*, *b* and $c_1 + c_2$ were determined using the extinction coefficients cited by Jeffrey and Humphrey (1975), modified for a 50 mm cell path-length, using their data for mixed phytoplankton populations. Conversion of chlorophyll concentrations from ug L^{-1} to mg m^{-2} was achieved by multiplying the area of the cores by the appropriate factor. Statistical analysis consisted of t-tests between the means obtained from each dilution (Zar, 1974).

Algal mat nutrient status

Ten cores of algal mat together with sediment (which was placed in Whirl Paks) were collected from the same points as those for algal mat dry weight analysis in March and April. For April this totalled five (positions) x ten (replicates) = fifty samples of algal cores for each sampling point containing algal mat. The ten replicates of mat for each position and the sediment were pooled, dried at 110 ^{o}C overnight and ground to a 0.5 mm particle size. Nutrient analysis was by Kjeldahl digestion for TN, and perchloric acid digestion followed by the single solution method for TP using the methods described by Atkins et al. (1978) for sediment.

The variation in dry weight of algal mat between sites necessitated the expression of the TN and TP content of sediments and mat in mg g^{-1} rather than g m^{-2}, but the latter was calculated for comparison on occasions. Statistical analysis consisted of pooling the five sets of ten replicates from each sampling point, and comparing their means for the algal mat. Sediment values are the expression of three sets of two replicates for each point. Nickol River sediment and mat TN and TP values are given for March only, as this study site was inaccessible in April.

Regrowth of mats in the field

In early March, at each sampling point containing mat along the transects at King Bay, Dampier Salt and Nickol River, a 1 x 1 m square was cut with a scalpel and peeled back, taking care to remove as little sediment as possible. The removed mat was transported away from each sampling point to minimize local disturbance of the algal mat. These areas were examined on later field trips (April/May and July). The 50 x 50 mm areas cleared in March for the small transects at King Bay were also examined on later field trips.

Nutrient inflow to King Bay

Fresh mangrove leaves (Rhizophora mangle) which had been dislodged from trees by strong winds at King Bay, were observed to be washed onto the algal mat at high tides. To measure the potential for nutrient release from these fresh (green) leaves, as compared with dry leaves which are normally carried onto the mat, samples of each were collected at the inlet to South King Bay. Fresh weights were obtained, and samples dried overnight at 110 °C and weighed after cooling in a desiccator. Total organic carbon was determined for six replicates by the methods described above. TN and TP were determined after grinding by the methods described for determination of nutrient status of algal mats.

Rehydration of dry algal mats

Excess sediment was scraped from ten replicates of 50 x 50 mm algal mat samples from King Bay that had been dry for four weeks. These were weighed, and this figure used to represent 'dry weight'. Each replicate was rehydrated by placing it in a 500 ml plastic container with 300 ml of standard seawater (36.4 °/oo) and removed, blotted dry and weighed at different times (from 0.5 to 60 min). They were then left to dry for five days, and the weight losses recorded. After 12 hours, five samples were placed in a glasshouse. The laboratory was at a constant temperature of 23 °C, and the glasshouse fluctuated from 12 °C to 35 °C.

Salinity and light trials

Salinity trials. These trials were set up to determine in the laboratory the effects on algal mat growth of a range of salinities and light levels.

Cores (160 from each site) of algal mat, each 19 mm diameter, were prepared from King Bay and Nickol River, trimmed of excess sediment and weighed into pieces of 1.0 0.5 g for King Bay and 1.0 0.2 g for Nickol River.

An artificial 'seawater' medium was prepared as described in Gordon et al. (1980), but without the vitamin block and trace metal additions as the algal cores were considered to have sufficient concentrations of these for the duration of the experiment. Twenty litres of this medium of 200 $^{o}/_{oo}$ salinity were prepared (Appendix 1), and diluted with deionised water to make two litres of seven salinity concentrations ranging from 20 $^{o}/_{oo}$ to 140 $^{o}/_{oo}$. Tap water was used to represent 0 $^{o}/_{oo}$ 'seawater'.

Ten cores of each mat were placed in 500 ml containers, and 300 ml of each salinity concentration added to make a series of two containers with each salinity (0 - 140 $^{o}/_{oo}$) for each site (King Bay and Nickol River). These containers were placed in a glasshouse (temperature range 12 ^{o}C - 35 ^{o}C) and randomized. To replace evaporative losses, deionised water was added every two to four days, maintaining the volume at 300 ml per container.

One core from each container (16 per site) was used to determine initial values of each parameter; for eight replicates the dry weight, organic carbon and chlorophyll $\underline{a}$, $\underline{b}$ and $\underline{c}_1 + \underline{c}_2$ were determined by the methods described previously under this section.

After 23 days, eight replicates from each salinity concentration were used for chlorophyll determination and the same number for rates of nitrogen fixation (Chapter 6), dry weight and organic carbon analysis. Two replicates were used for taxonomic study (Chapter 3).

Light trials. An artificial seawater medium was prepared (Appendix 1) and modified to 60 °/oo. One hundred algal cores were prepared from King Bay mat by the methods already described in this section. Ten replicates were placed in each of ten, 500 ml plastic containers, and 300 ml of seawater medium added to each.

Three levels of shading were achieved under outside conditions by wrapping 50%, 75% and 90% shadecloth around wire frames and placing two containers of mats under each. Two containers were placed in full light and two in total darkness, which was achieved by placing one container in a light-tight box under outside conditions and one in the dark under laboratory conditions to minimise heating.

To obtain base line data for this trial, samples collected initially were analysed for chlorophyll, dry weight and organic carbon, as described earlier.

Harvesting was undertaken after 42 days and the cores from each light level analysed for nitrogen fixation rates (Chapter 6), chlorophyll, dry weight and organic carbon.

4.3 RESULTS

Groundwater

Salinity. Subsurface salinities were high at all sites (Table 4.1) particularly at Dampier Salt where 200 °/oo was exceeded. They were generally lower outside the algal mat zone and a gradient from high to lower salinity occurred from the mat centre toward the mangroves. Halophytes were present in areas with salinities of 80-90 °/oo. A reduction of these concentrations occurred from March to April, and measurements taken a few days apart in April were quite variable (Table 4.1).

Table 4.1 Groundwater salinities at King Bay, Dampier Salt and Nickol River.

KING BAY

Sample Point (see Fig. 2.3)	Distance Along Transect (m)	Salinity (°/oo) 05.03.83	25.04.83	26.04.83	Comments
	20	-	134	-	
1	60	130	112-122	108	
2	98	145	-	-	
	100	-	156-160	155	
3	102	135	-	-	Algal mat start
4	145	155-157*	-	144-152	
	150	-	162	-	
5	175	150	-	150-156	
	180	162	156-158	-	Algal mat end
6	193	80	-	76-93	
	200	-	70	-	Avicennia zone starts
	300	-	52	-	

* When a range of salinities is given a number of replicates were taken.

DAMPIER SALT

Sample Point (see Fig. 2.4)	Distance Along Transect (m)	Salinity (°/oo) 07.03.83	26.04.85	01.05.83	Comments
1	0	155	-	129-139	
	5	180	162	-	
2	10	205-210	197	178-189	Algal mat start
	30	215	-	-	
3	50	210-220	177	152-169	
	80	173	-	-	
4	110	175	164-166	152-154	
	155	160	-	-	
5	200	142	110-112	124	Patchy mat distribution
	220	105	-	-	Algal mat end
6	240	95	62	94-96	Halophytes
	250	82	-	-	present

NICKOL RIVER

Sample Point (see Fig. 2.5)	Distance Along Transect (m)	Salinity (°/oo) 03.03.83	Comments
1	1	95	
2	10	115-120	Algal mat start
3	30	93	
4	110	130	
5	160	125	
6	300	94-98	Algal mat end
7	340	88-92	Halophytes present

Water left by the tide at King Bay and Nickol River ranged consistently from 50 to 60 $^{o}/_{oo}$ even though groundwater concentrations in adjacent areas (less than a metre away) were 100 to 130 $^{o}/_{oo}$. Groundwater salinities remained at these levels over successive tidal cycles in King Bay. The ponded water brought by tides at Dampier Salt persisted at 60 $^{o}/_{oo}$ when present in March and throughout the observation period in April/May. At all sites tidal water usually entered the tidal flat at a salinity of 40 $^{o}/_{oo}$ and left at 60 $^{o}/_{oo}$.

Metal cations. The concentrations of metal ions at Dampier Salt were higher in groundwater directly under the algal mat, particularly in the central area (Figure 4.1). Few differences however, existed between the sampling points when the cation proportion was compared (Table 4.2a). The average proportion of cations in the groundwater was similar to that found in seawater of normal salinity, except for calcium, which was higher in the groundwater. The Mg/K ratio in groundwater was considerably higher than seawater or bitterns (Table 4.2b), although the salinity concentrations at the sampling points lay between salinity values of seawater and bitterns discharge water.

Nutrients. In general at all sites, nutrients in groundwater occurred in lower concentrations under the mat than at the seaward or landward ends of the transect. In April, groundwater NH_4-N concentrations were higher (50 - 100 ug L^{-1}). The quantities of nitrate were extremely high at all sites, the concentration varying from 3,000 to 20,000 ug L^{-1} NO_3-N). In March, similar concentrations were present at each site, and in April this had increased two-fold at King Bay and Dampier Salt. Groundwater TN content followed a similar pattern to nitrate at all sites for March and April.

Table 4.2a A comparison of sampling point groundwater cation content with seawater cation content along a transect at Dampier Salt.

Sample Point	% of Cation Compared To The Sum (Na + Mg + K + Ca) of Ions Measured			
	Na	Mg	K	Ca
1	86.4	11.1	1.9	0.6
2	87.1	10.2	2.5	0.2
3	87.8	9.3	2.6	0.3
4	87.3	8.6	3.0	1.1
5	87.9	9.6	1.8	0.7
6	86.8	9.9	2.0	1.3
seawater	84	10	3	3

Table 4.2b A comparison of sampling point groundwater Mg/K ratios with seawater and bitterns discharge water Mg/K ratios.

Sample Point	Mg/K Ratio	Salinity (^{o} /oo)
1	5.7 : 1	155
2	4.1 : 1	210
3	3.5 : 1	220
4	2.9 : 1	175
5	5.4 : 1	142
6	4.9 : 1	95
seawater	3.3 : 1	35
bitterns	2.8 : 1	275

The concentrations of PO_4-P and TP at all sites were below 400 ug L^{-1} in March and April.

Algal mat dry weight and organic carbon content

March. The water content of the algal mats ranged from 29.2% at Dampier Salt to 47.6% at Karratha (Table 4.3) and the dry weights in March ranged from 1.76 x 10^3 g m^{-2} (Dampier Salt 'wet' mat) to 6.64 x 10^3 g m^{-2} (Karratha) (Table 4.3). The highest organic carbon occurred in King Bay (0.76 x 10^3 g m^{-2}) but highest percentages were obtained from Dampier Salt (Table 4.3).

Friable samples of mat from King Bay contained similar percentages of organic material to those of Dampier Salt. This represents a reduction from the normal mat at Dampier Salt of 1-10% organic matter, and an increase of 10% at King Bay.

Algal mat adjacent to the tidal creek in King Bay had a relatively low dry weight (Figure 4.2), but at one metre from the creek the dry weight was higher than in the mat 4-7 m away. Organic matter was consistent over the transect except for a slight reduction adjacent to the creek.

Algal mat dry weights at Nickol River were similar to King Bay and varied from 2.33 x 10^3 g m^{-2} to 4.32 x 10^3 g m^{-2} (Table 4.3), with lower values occurring at the landward edge of the algal mat.

April. In April, dry weights from sets of samples at sampling points at King Bay were quite variable ($F = 9.102$, $p < 0.0001$, Figure 4.3), but there was less variability in those measurements from point 4 ($F = 1.886$, $p = 0.1293$). While there was little difference between dry weights at these points there was a higher amount of organic carbon at point 4 ($t_5 = 3.576$, $p < 0.05$).

Table 4.3 Percentage water content, dry weight and total organic carbon content of algal mats collected from four sites in March, 1983.

Parameter	F Value *	Probability	Nickol River	Karratha	King Bay	Dampier Salt 'dry'	Dampier Salt 'wet'	Friable Mat King Bay	Friable Mat Dampier Salt
% Water Content	87.6	<0.001	46.3 (0.54)	47.6 (0.63)	36.7 (1.2)	40.9 +[1] (0.57)	29.2 (0.37)	-	-
Dry Weight ($\times 10^3$g m^{-2})	97.5	<0.001	4.32 +[2] (0.17)	6.64 +[3] (0.33)	4.15 (0.20)	1.91 (0.12)	1.76 (0.10)	-	-
Total Organic Carbon ($\times 10^3$g m^{-2})	45.3	<0.001	-	-	0.760 (0.03)	0.650 (0.03)	0.551 (0.04)	-	-
% Organic Matter	-	-	-	-	13.23 +[4] (0.24)	36.8 +[5] (0.90)	27.31 (1.3)	23.0	26.6

* F values given are derived from ANOVA between all sites and t-statistics from between means of each site.
Each figure is represented as mean (standard error).
'-' denotes parameter not measured.

+[1] t = 12.23 $p < 0.001$, between adjacent means
+[2] t = 6.151 " "
+[3] t = 6.401 " "
+[4] t = 10.36 " "
+[5] t = 5.9 " "

Dampier Salt generally had much lower dry weights (2.5×10 g m^{-2}) than King Bay, but organic carbon content was approximately the same. The area nearest the levee wall had the highest dry weights and organic carbon than other points on the transect (Figure 4.4). Percentage organic matter was higher in central areas of the mat than at its edges.

Algal mat chlorophyll content

Algal mat chlorophyll *a* content in March varied at each site from 50 to 200 mg m^{-2}, and there were measurable quantities in sand and sediment not colonised by algal mat (Figure 4.5). In April, the quantities of chlorophyll *a* doubled at King Bay and Dampier Salt (Figure 4.6). The ratios of chlorophyll *a*, *b* and $c_1 + c_2$ changed along each transect in March, but this was not so apparent in April (Figure 4.7); chlorophyll *a* was generally greater than chlorophyll $c_1 + c_2$ which in turn was greater than chlorophyll *b*.

At King Bay, quantities of chlorophyll *a*, *b* and $c_1 + c_2$ varied little at transect point 3 ($F = 2.048$, 0.3763, 0.1296 respectively, all not significant), chlorophyll *a* and *b* levels were higher towards the tidal creek (Figure 4.7). Dampier Salt showed higher concentrations of chlorophyll *a* at the first transect point (2) but reduced values at the others; chlorophyll *b* and $c_1 + c_2$ varied little over the transect (Figure 4.7).

Algal mat nutrient content

The total nitrogen (TN) concentration in the algal mat in King Bay was significantly higher closer to the tidal creek (3.65 mg g^{-1} mat) than further away (2.25 mg g^{-1} mat, $t = 3.992$, $p < 0.004$, Figure 4.8) and much greater than in the sediments ($t = 10.61$, $p < 0.001$). Phosphate levels were very much lower than nitrogen levels (0.299 - 0.347 mg g^{-1} mat) and not significantly different along the transect areas. Phosphate levels in the

mat were significantly higher than in the sediment below it (point 3: $t = 4.723$, $p < 0.001$ and point 4: $t = 3.078$, $p < 0.015$). Sediment levels of TN and TP were similar close to the tidal creek and further away.

A similar pattern was found in Dampier Salt (Figure 4.8); phosphate concentrations of the mat did not vary over the transect ($F = 0.3545$, $p < 0.787$), and similar amounts were present at each point (0.350 - 0.391 mg g^{-1} mat). These concentrations were marginally higher than in the sediments beneath them, except at the most seaward point (5). TN content was higher in the mat at all points than in the sediment, and higher values occurred in the middle portion of the algal mat (Figure 4.8). These values were greater than those found in King Bay. Sediment TN values varied little over this transect.

At Nickol River, high TN values were observed in the mat and corresponding large values were present in the sediment below it (Figure 4.8).

Friable mat from Dampier Salt and King Bay had similar levels of phosphorus to unfriable mat but a quarter of the nitrogen (0.7 mg g^{-1} at King Bay and 2 mg g^{-1} at Dampier Salt).

Regrowth of mats in the field

Large areas (1 x 1 m) cleared at King Bay in March had not been recolonised after eight weeks, but the smaller areas cleared for the minor transects (Figure 4.2) had recolonised lightly. After 17 weeks, some regrowth had occurred in 1 x 1 m quadrats but this was relatively minor, and crab burrows were present within the cleared areas.

All cleared areas at Dampier Salt had regrown mat after eight weeks except for point 2 which, like the surrounding area, was covered by dust, apparently derived from levee 24 (Figure 2.4).

Cleared areas at Nickol River sampling points had also grown mat after eight weeks.

Nutrient inflow to King Bay

There was little difference in the organic carbon content of fresh and dry Rhizophora leaves, though there were significantly lower amounts of nitrogen and phosphorus in the dry ones (Table 4.4). The C:N:P: ratios of these leaves were equal with regard to N and P, but carbon was proportionately twice as high in dry leaves as in fresh.

Mat temperature

Temperatures on the algal mat surface ranged from 37 - 42 ^{o}C at all sites and were generally 2 - 4 ^{o}C lower at a depth of 20 mm into the mat.

Rehydration of dry algal mats

The weight of dry mats increased by 8% after 30 seconds immersion in water, and 12% after five minutes, but little further gain occurred after one hour (Figure 4.9a). Forty percent of this water was lost after 18 hours in the glasshouse, and less than 30% in the laboratory (Figure 4.9b). Subsequently water loss was minimal for all mat samples and only on one day was there a significant difference in water loss between the two environments.

Salinity trials

There was little change in either dry weight, organic carbon or percentage organic matter of King Bay algal mat cores subjected to the range of

Table 4.4 Carbon (C), nitrogen (N) and phosphorus (P) content of fresh and dry leaves of Rhizophora mangle taken from South King Bay.

Parameter Measured	Fresh Leaves	Dry Leaves	Significance
Water content (% fresh weight)	64.3	23.2	-
Total organic carbon ($g\ kg^{-1}$)	783 ± 5*	845 ± 43	NS
Total nitrogen ($g\ kg^{-1}$)	6.65 ± 0.17	3.53 ± 0.25	$p < 0.0005$ $t = 14.07$
Total phosphorus ($g\ kg^{-1}$)	0.710 ± 0.006	0.347 ± 0.016	$p < 0.0001$ $t = 21.49$

C:N:P ratio (fresh) = 1100:9:1

C:N:P ratio (dry) = 2400:10:1

Statistics shown are from t-tests between means of 6 replicates.

* standard error.

salinities (Figure 4.10). A loss in dry weight and a subsequent increase in organic carbon at salinities greater than 20 °/oo occurred in cores from Nickol River (Figure 4.11). There was a 5 to 40% increase of organic matter in these cores.

Chlorophyll *a* in algal cores from King Bay increased by at least 100 mg m^{-2} in all salinities (Figure 4.12). Chlorophyll *b* and $\underline{c}_1 + \underline{c}_2$ increased in salinities above 80 °/oo. Algal cores from Nickol River followed a similar trend; chlorophyll *a* increased by at least 50 mg m^{-2} (Figure 4.13), the largest increase being found at 80 °/oo where 170 mg m^{-2} (7.4 mg m^{-2} d^{-1}) had been added to the original content after 23 days. Chlorophyll *b* and $\underline{c}_1 + \underline{c}_2$ decreased slightly by 0 - 10 mg m^{-2} in all salinities except 100 °/oo (Figure 4.13).

Light trials

There were no apparent trends in algal core dry weight, organic carbon or percentage organic matter after 42 days growth at different light intensities. Chlorophyll *a* increased at 90% shade and total darkness, but not significantly. Losses in chlorophyll *b* (Figure 4.14) occurred under all light conditions. Chlorophyll $\underline{c}_1 + \underline{c}_2$ increased only in 90% shade.

4.4 DISCUSSION

Groundwater

The stability of groundwater salinity concentrations over successive tidal cycles indicates that there was little short-term exchange between groundwater and tidally-transported marine water. Algal mats occur on the sediment surface, and this suggests that groundwater could have little direct influence on mat growth. Rooted macrophytes (halophytes and mangroves) however, may have their distribution dictated by groundwater

characteristics, such as salinity (Table 4.1, Gordon, 1983). The only influence that groundwater is likely to have on algal mats is therefore indirect, for example if rooted macrophytes influence algal mat growth by shading or in some other way.

There was little evidence to indicate that algal mats influenced the nutrient concentration of sediments directly beneath them (Figure 4.8), although high nitrate concentrations in groundwater below mats suggest that leaching of nitrate may have occurred. Rainfall occurred between March and April, and during this time groundwater nitrate concentrations doubled at King Bay and Dampier Salt. This, and the decrease of groundwater salinity over these times at both sites (Table 4.1), supports the view that nitrate may have been leached from the mat. An alternative interpretation is that rainfall leached nutrients from the mudflat inland of the mat, and the groundwater had carried these to the coast. Nitrate-rich groundwaters are known to occur in adjacent localities (Australian Water Resources Council, 1983).

The similar ratio of major cations in Dampier Salt groundwater and seawater (Table 4.2) supports the view that the groundwater immediately below the mat was essentially marine water, which had leached through surface sediment (see Chapter 5), after ponding and evaporative concentration on the algal mat (Figure 4.1), rather than from bitterns derived from evaporative ponds further inland.

Light

In the Dampier Archipelago, where all of the algal mats studied were non-heterocystous, no mats have been observed in shaded conditions. Data from

the light trial are inconclusive (Figure 4.14); if algal mats were prevented from growing within mangrove stands by low light levels, then in this trial higher growth rates would have occurred in full light than in shade; this was not observed.

There is evidence that the metabolic processes of algal mats are limited by high light levels (Stewart et al., 1978; Reynaud and Roger, 1981; Stal et al., 1984). Light tolerance in algal mats is, however often closely related to ambient temperature (Jones, 1977b, 1977d) - an important consideration when algal mats occur from the Antarctic (Parker and Simmons, 1981) to tropical environments (Stewart et al., 1978). Further study is required before conclusions can be made on the effect of light on long term algal mat growth in the Dampier Archipelago.

Dry weight and organic carbon

One reason for measuring the organic carbon content of algal mats is to provide a measure of the quantity of algal material in the mat, in relation to sediment, so that mat characteristics can be related to the hydrologic regime in which it grows. Similar amounts of organic carbon were present at King Bay and Dampier Salt (Table 4.3, Figure 4.3, 4.4), and the percentage of organic carbon at both sites was similar to that reported in other algal mat systems (Bauld, 1981a). The higher levels of organic carbon at the point closest to the tidal creek in King Bay (Figure 4.3) suggests that more growth had occurred there, presumably because water availability was higher than at more landward points. Organic carbon decreased within one metre of the tidal creek (Figure 4.2), and this may have been caused by tidal erosion (Chapter 2).

The percentage of organic matter in King Bay algal mats was much lower than at Dampier Salt (Table 4.3), indicating that more sediment was trapped at King Bay by the growing cyanobacteria. The lack of regrowth in large, cleared areas, and growth in smaller ones, indicates that variables such as sediment instability, faunal burrowing and sediment influx were important factors determining local algal mat distribution. The distribution of mat in King Bay, and its variability over short distances (Figure 4.3), supports this view. Therefore sediment instability, rather than reduced light, may reduce development of mats on mangrove-associated sediments.

The higher percentage of organic matter (i.e. less sediment in the algal mat) at Dampier Salt (Table 4.3) supports the observation that there was less vigorous water movement here than at King Bay. At Dampier Salt, the high dry weight and the low percentage of organic matter found in algal mat close to the levee wall (Figure 4.4) indicates that a greater amount of sediment was being combined into the algal mat here. This was likely to be caused by dust blowing into the algal mat in this area. The higher carbon content of this mat, compared to other areas at Dampier Salt, may therefore be a response to dust smothering the mat surface and subsequent regrowth.

The marginal increases in algal mat dry weight and organic carbon in the salinity trial (Figure 4.10, 4.11) suggest that these measurements were not true indicators of metabolic activity. The high nitrogen content of the algal mat at King Bay (16.5 g $N\ m^{-2}$) and Dampier Salt (14 - 21 g $N\ m^{-2}$, Figure 4.8), and high chlorophyll production (described below) indicate high metabolic activity (Chapter 6), while constant biomass suggests high turnover.

The occurrence of nutrient leakage, including carbon loss, during cyanobacterial growth and cell death is well known (Ward and Wetzel, 1975; Jones and Wilson, 1978). The small change in biomass at King Bay and Dampier Salt expressed as organic carbon content, suggests that the algal mats were growing inefficiently, with the potential for the carbon, nitrogen and phosphorus contained within them to leach out.

Chlorophyll

Although there was little increase in carbon or dry weight at King Bay and Dampier Salt from March (Table 4.3) to April (Figure 4.3, 4.4), chlorophyll _a_ values almost doubled at both sites (Figure 4.6). Constant species composition at Dampier Salt may explain the similar chlorophyll _b_ and _c_ values in both months. In King Bay there were high values of chlorophyll _c_ in March (Figure 4.5) and increases of this and chlorophyll _a_ in April (Figure 4.6). The pigment differences between King Bay and Dampier Salt reflect their species composition (Chapter 3). Thus, the changes at King Bay from March to April may be considered to be both a change in composition, particularly diatoms (Jeffrey, 1968; Jeffrey and Vesk, 1981; Sammy, 1983), and an increase in cyanobacterial chlorophyll _a_ in the wetter months. The gain of chlorophyll _a_ at Dampier Salt which had a solely cyanobacterial composition, from March to April (Figure 4.6), supports this view.

The decrease in chlorophyll _b_ and _c_ at salinities below 80 $^{o}/_{oo}$ in King Bay mats (Figure 4.12) must be caused by the reduction in the populations of algae belonging to at least two classes, as no one class has both pigments, and only the flagellated Chlorophyta and Euglenophyta have chlorophyll _b_ (Jeffrey and Vesk, 1981). It follows that part of the increase in chlorophyll _a_ above 80 $^{o}/_{oo}$ is not caused by cyanobacterial growth. Nickol

River algal mats showed general losses of chlorophyll b and c over the range of salinities examined (Figure 4.13), and a peak of chlorophyll a production in the range 20-80 °/oo. This indicates that cyanobacterial chlorophyll a production was possible over this range.

Temperature and water loss

Algal mat surface temperature was high and only moderately reduced 20 mm into the mat. Despite this, the water content of these mats (29 - 47%, Table 4.3) was high when compared with mats in other terrestrial habitats (Jones, 1977a). The discovery that mats could rapidly absorb water, and lose it slowly (Figure 4.9), indicates a behavioural adaptation which is an advantage in an arid environment. Unbroken mats in the field hold around 40% of their dry weight in water; if any breaks occur, loss of water may be rapid and produce friable, dry portions on the mat edges. These portions may hold 1/4 to 1/3 of the nitrogen content of unbroken mats and consist of 23 - 26% organic carbon. Thus friable mat may be a source of loss of nitrogen and carbon from the system.

Mangrove litter

The nitrogen and phosphorus content of dry Rhizophora leaves was lower than in fresh leaves (Table 4.4), indicating that there was a potential for nutrient influx into the mat from fresh leaves. Frequent inundation of King Bay (Chapter 5) however, probably prevents mangrove leaves from being resident on the algal mat long enough to constitute a significant source. There may be other areas however, where leaves do provide a nutrient input to the mat.

4.5 SUMMARY

- Degree of tidal inundation (consistency and force) and salinity appear to be the main parameters affecting the algal mat structure and carbon content; water availability and sediment influx affect mat distributon within a system.
- Small variations in organic carbon content occurred at King Bay. There was even less variation at Dampier Salt, possibly because of its more constant and less energetic hydrologic regime.
- The hydrologic regime also determines recolonization in cleared areas of algal mat. Where tidal energy was great eg. King Bay, recolonization was slower than in less energetic areas like Dampier Salt and Nickol River.
- Salinity tolerances shown by the algal mats from King Bay and Nickol River indicated that mats could survive in high salinities in the field.
- Mats were able to conserve moisture at high temperatures when the surface was unbroken. Localized discontinuities produced friable portions of mat with one third to one quarter of the nitrogen content, and approximately 25% of the organic carbon, of normal mat. Thus nutrient loss may occur at sites where the mat is broken.
- Algal mats had high nitrogen (14 - 21 g $N\ m^{-2}$), phosphorus (0.7 - 1.5 g $P\ m^{-2}$) and carbon (500 - 800 g $C\ m^{-2}$) contents.
- Mats had a high metabolic activity (7.4 mg chl *a* produced $m^{-2}\ day^{-1}$) in optimal conditions, but this activity was not reflected in measurable organic carbon or dry weight increases, indicating a balance between growth and decay.

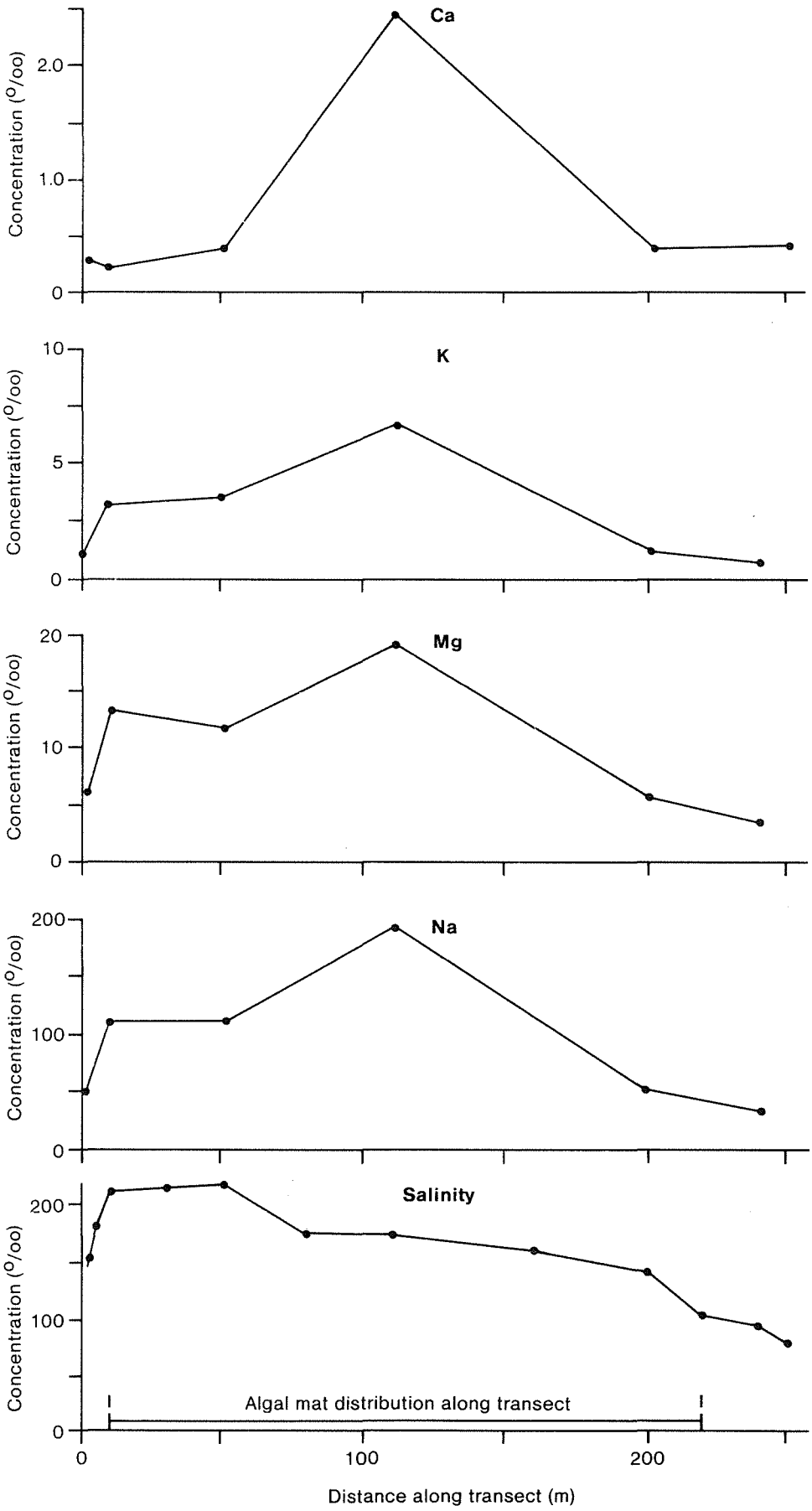


Figure 4.1 Concentrations of major cations in ground water collected along a 250m transect at Dampier Salt (see also Figure 2.4).

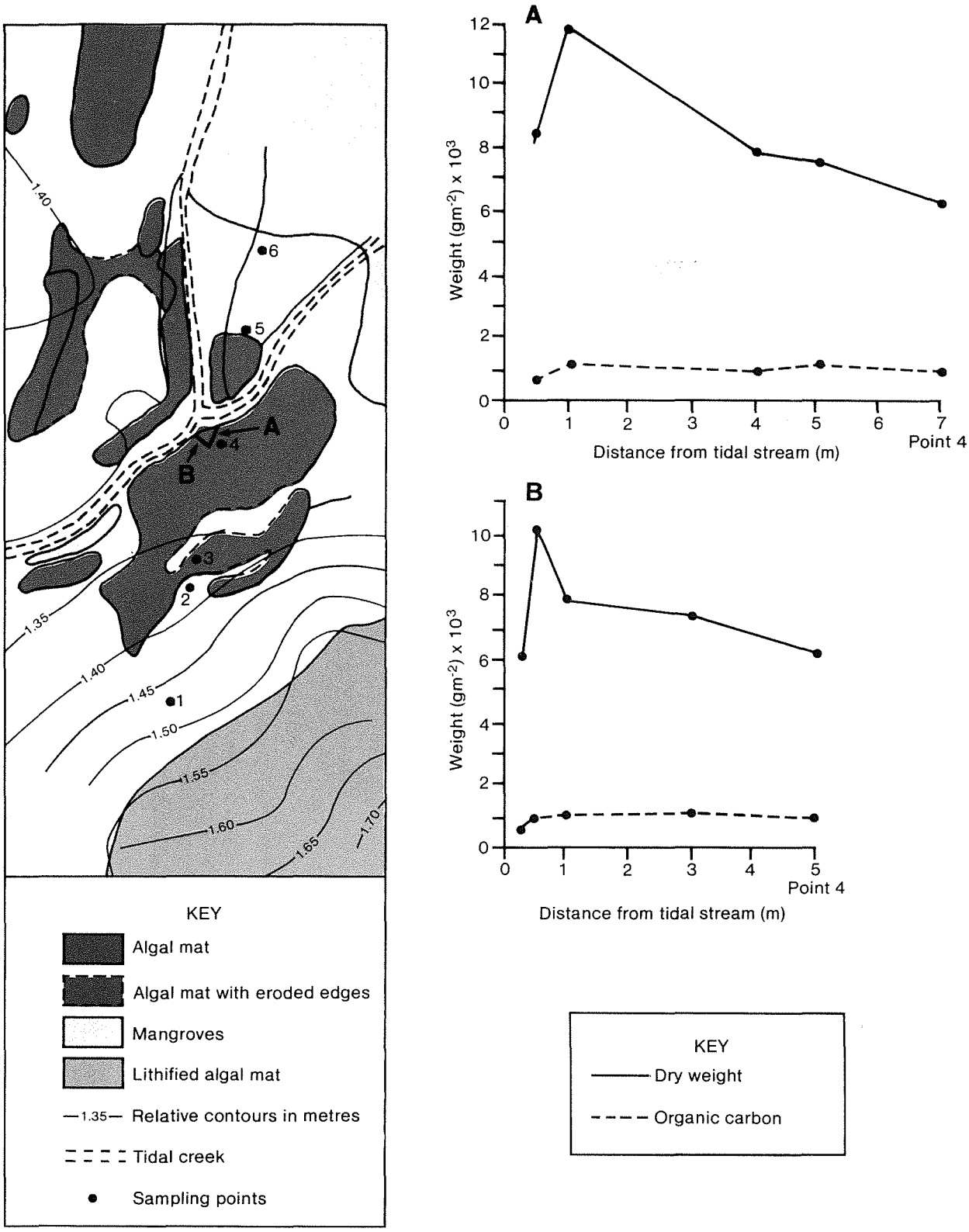


Figure 4.2 Dry weight and total organic carbon of algal mats on transects from sampling point 4 at King Bay in March.

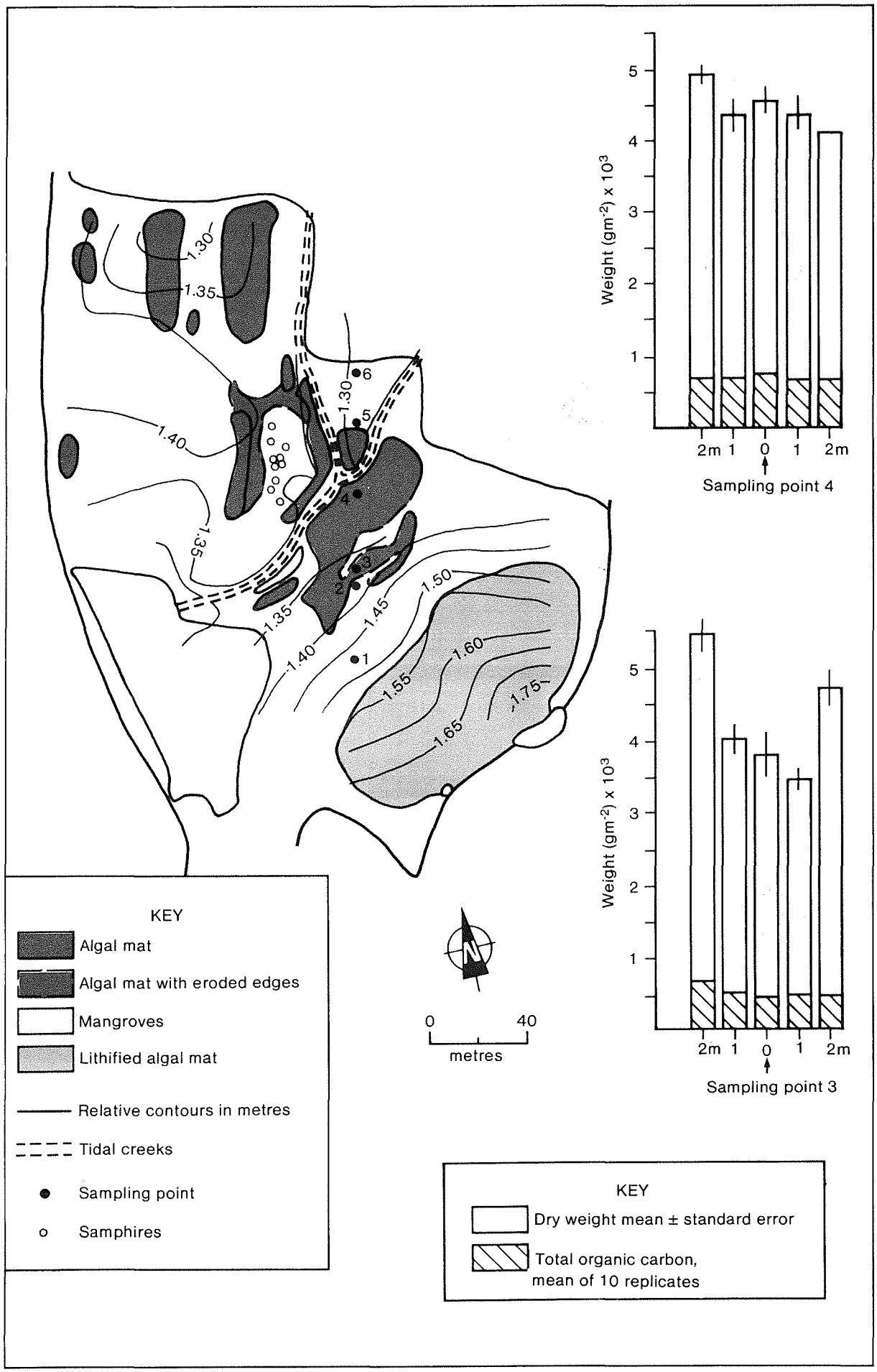


Figure 4.3 Dry weight and total organic carbon in algal mat from sampling points at King Bay in April.

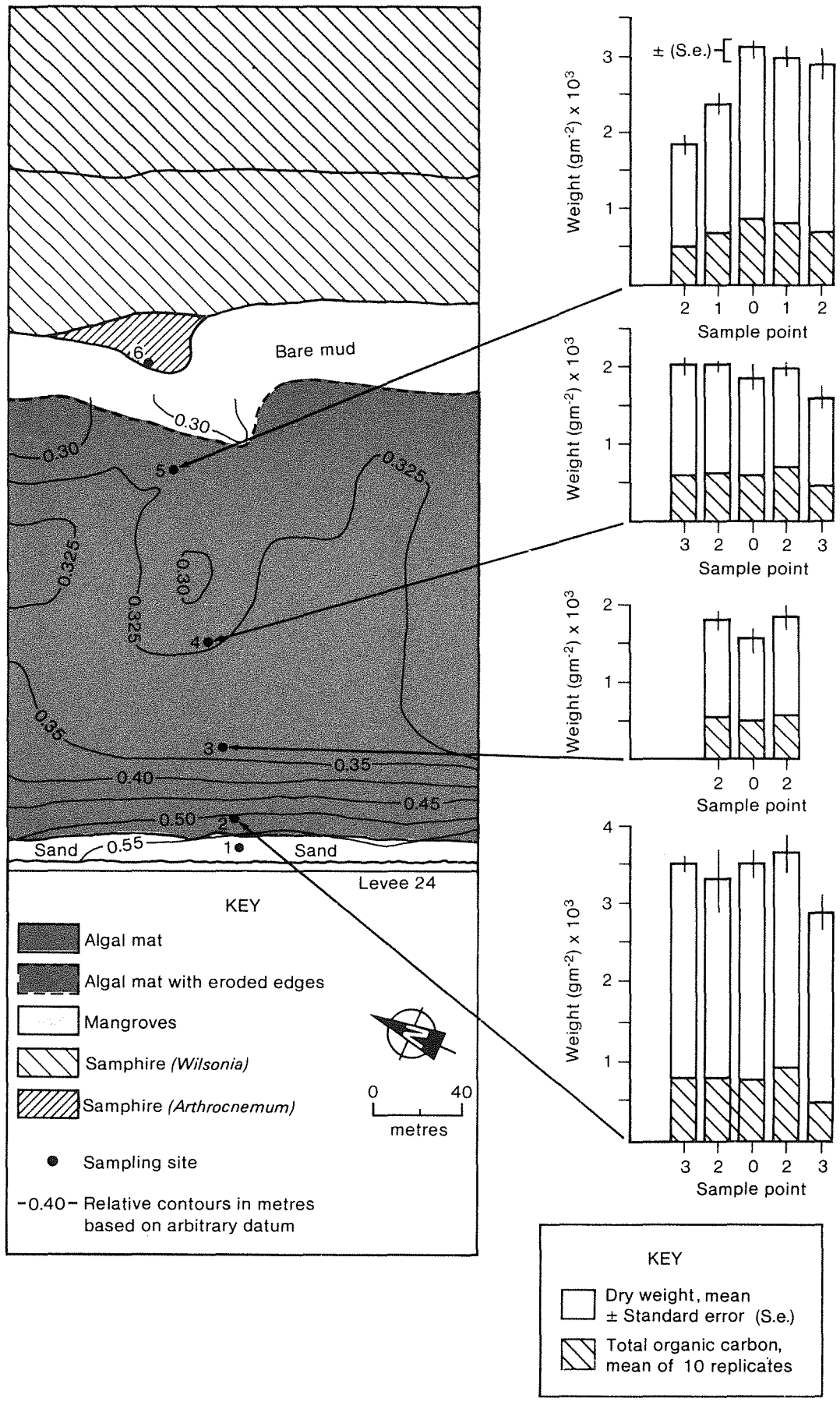


Figure 4.4 Dry weight and total organic carbon in algal mat from sampling points at Dampier Salt in April.

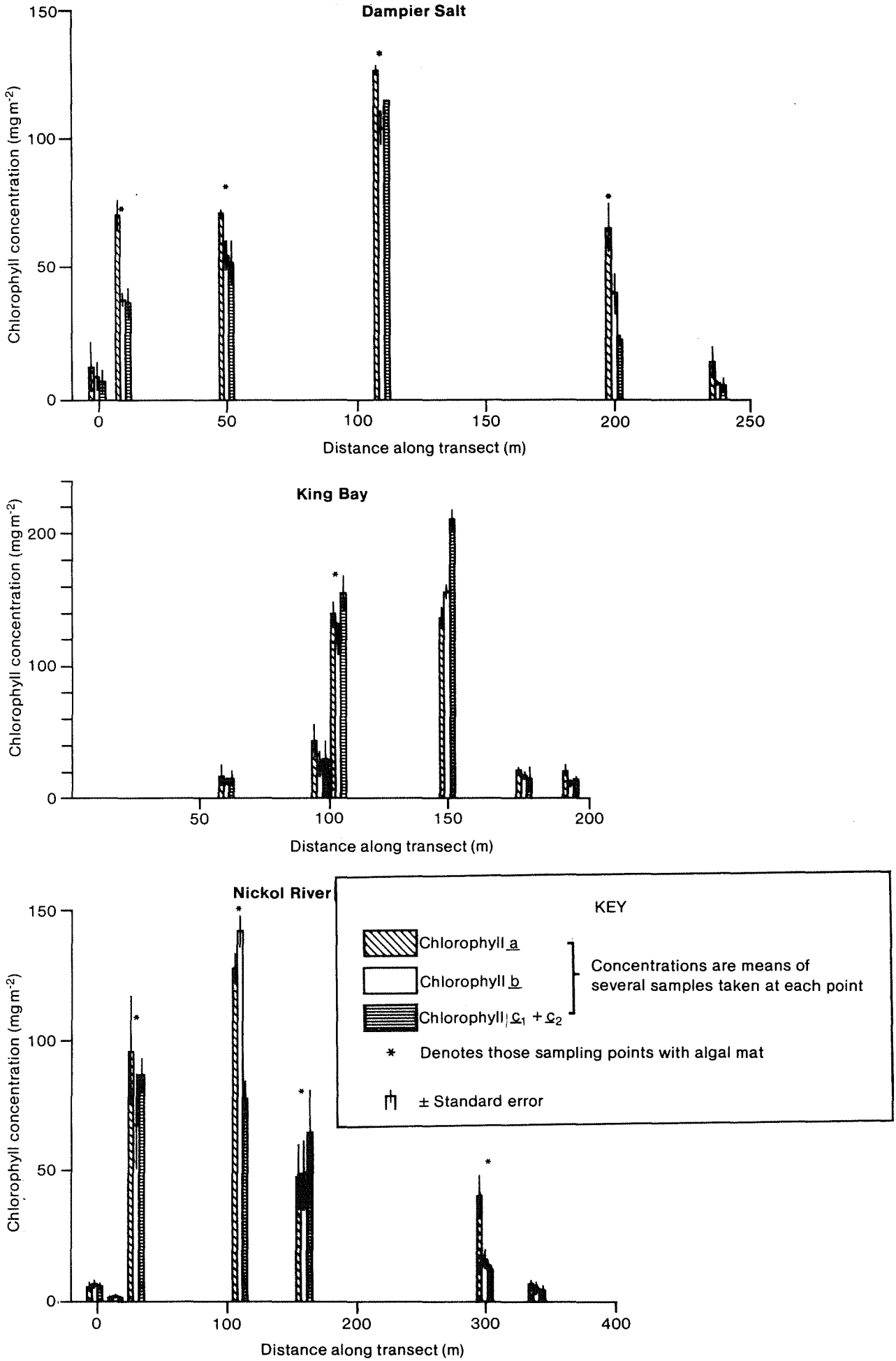


Figure 4.5 Algal mat chlorophyll content along transects at Dampier Salt, King Bay and Nickol River in March.

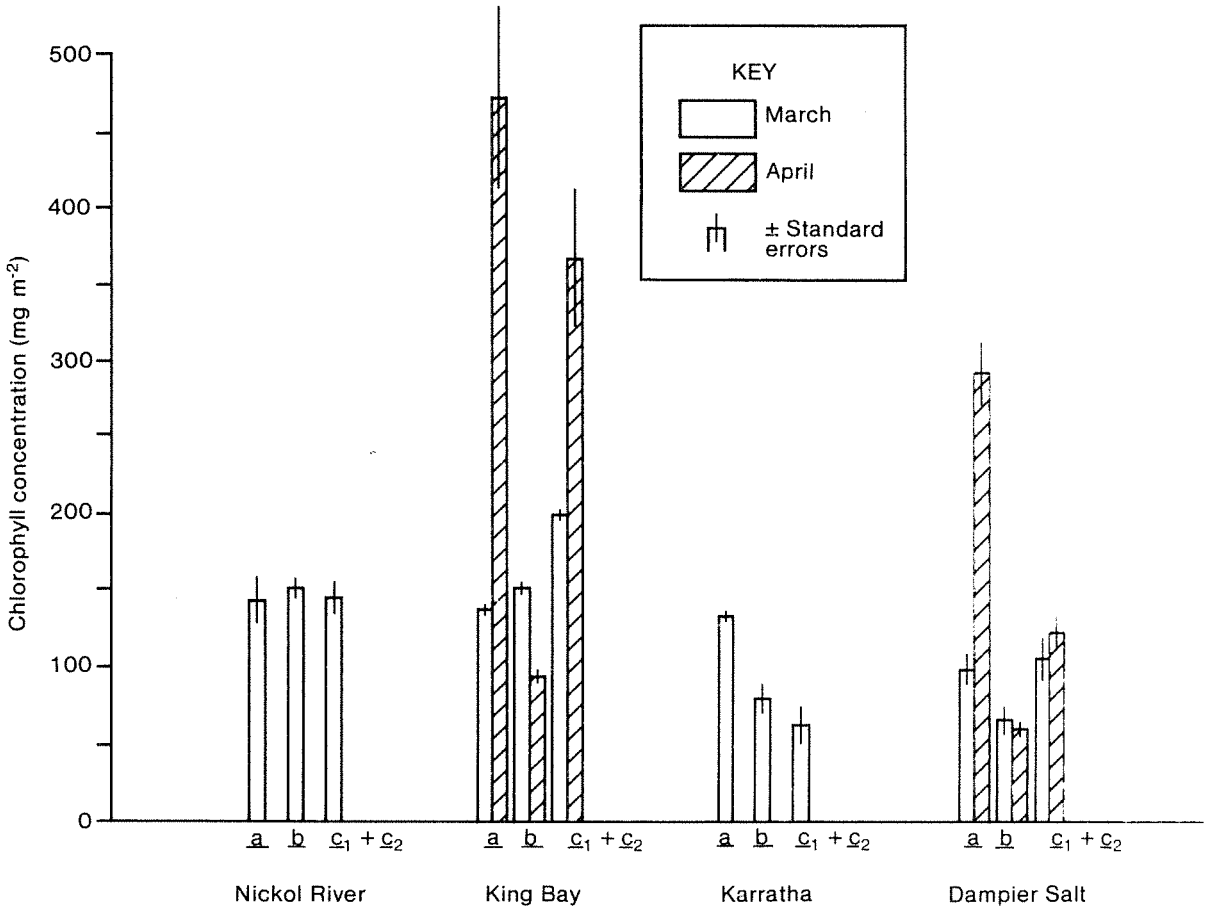


Figure 4.6 Chlorophyll concentrations in algal mat from each study site (March) and King Bay and Dampier Salt (April).

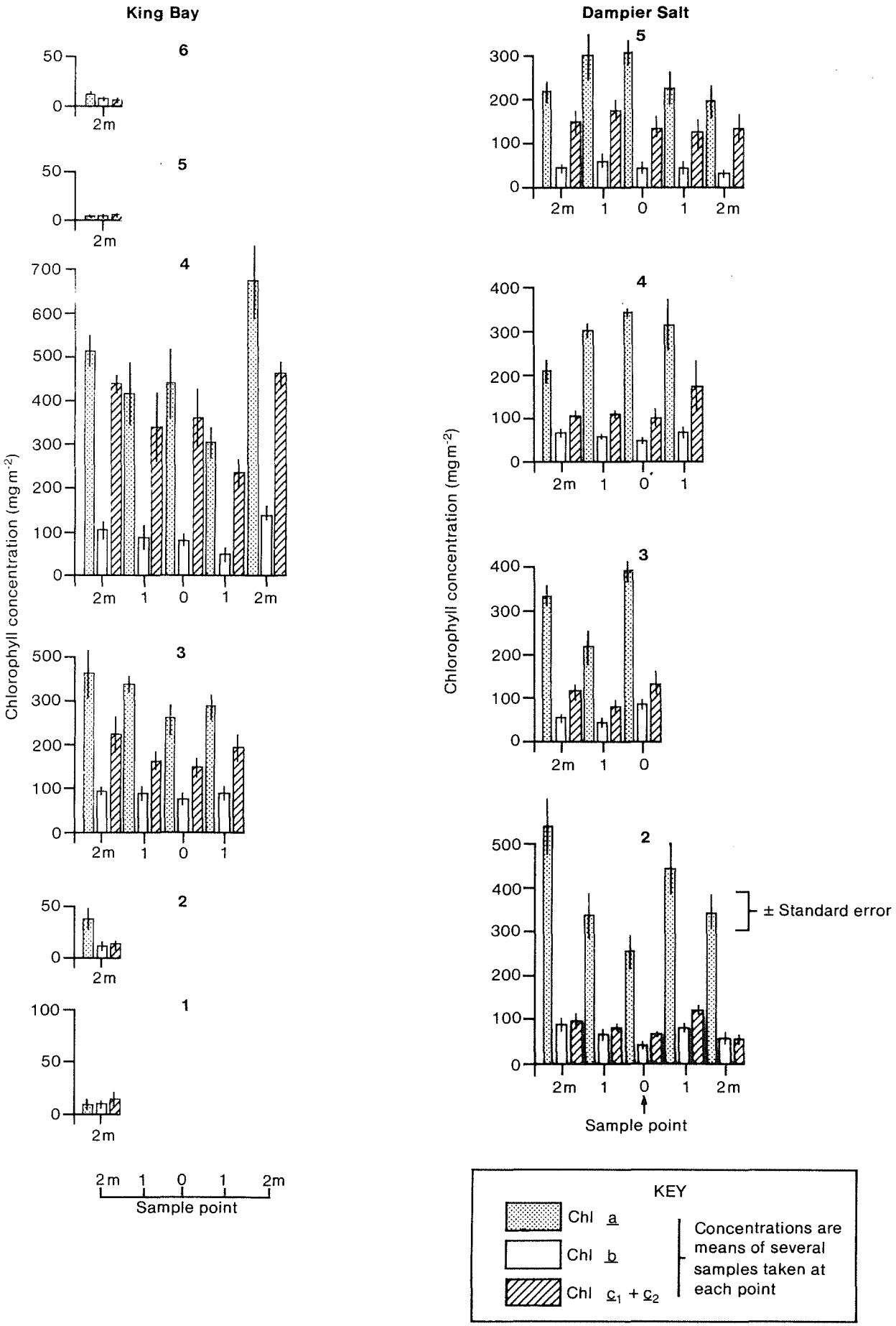


Figure 4.7 Algal mat chlorophyll concentrations at each sampling point along the King Bay and Dampier Salt transects in April.

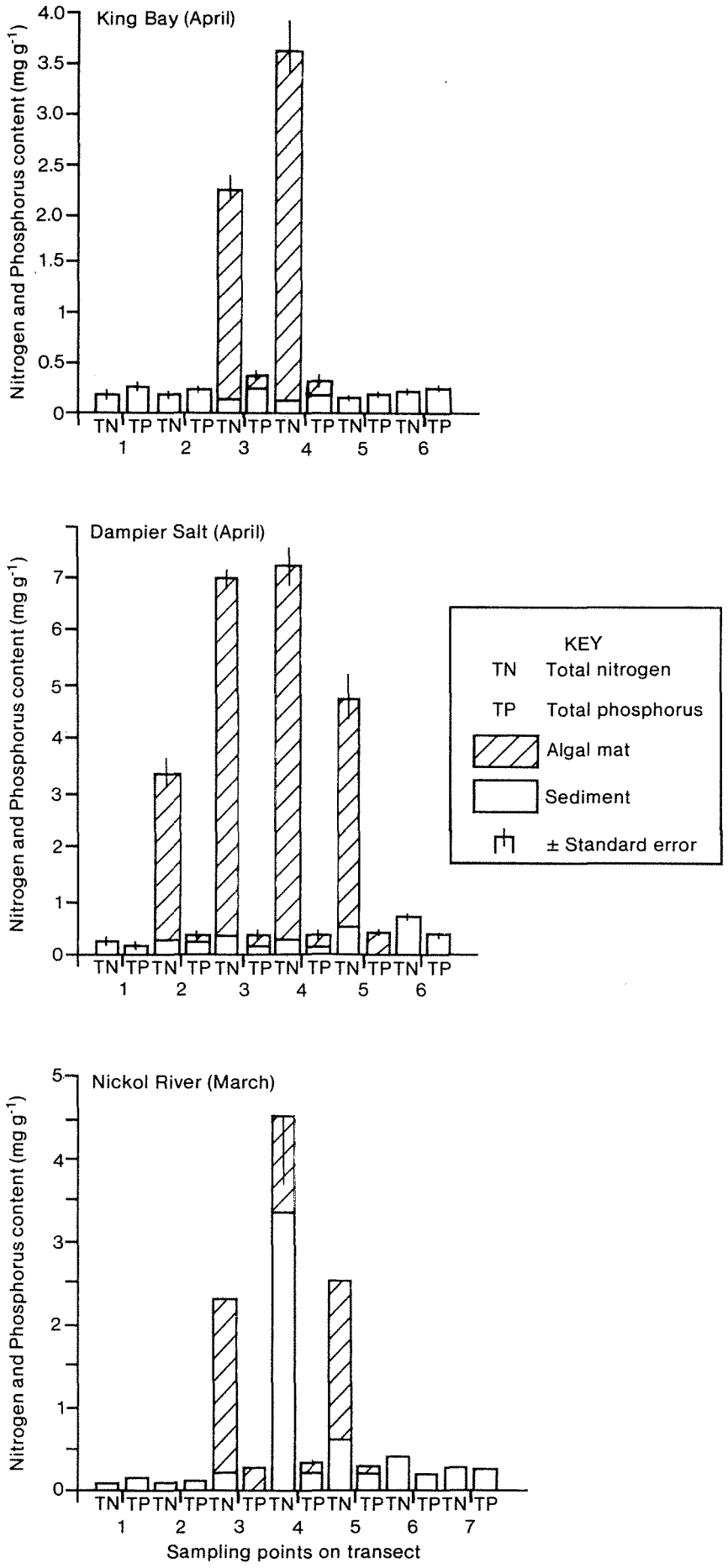


Figure 4.8 Total nitrogen and total phosphorus content of sediments and algal mat at King Bay and Dampier Salt in April, and Nickol River in March.

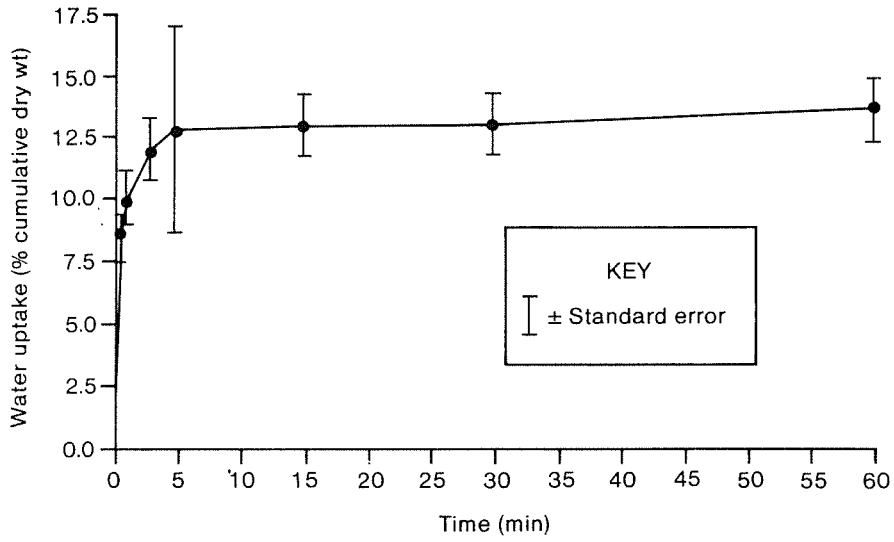
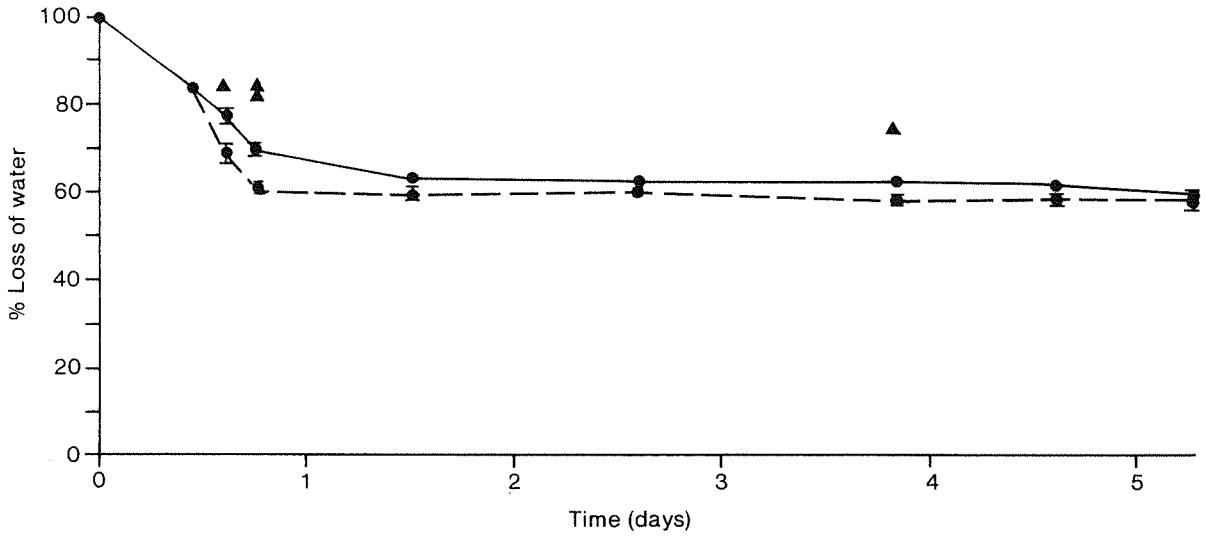


Figure 4.9a Water uptake by algal mats placed in seawater.



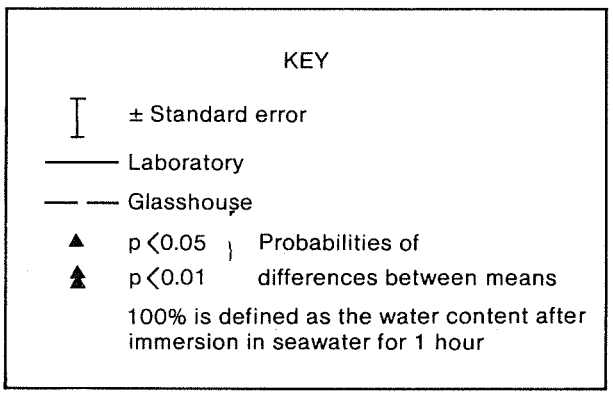


Figure 4.9b Water loss from rehydrated algal mat placed in a glasshouse and laboratory.

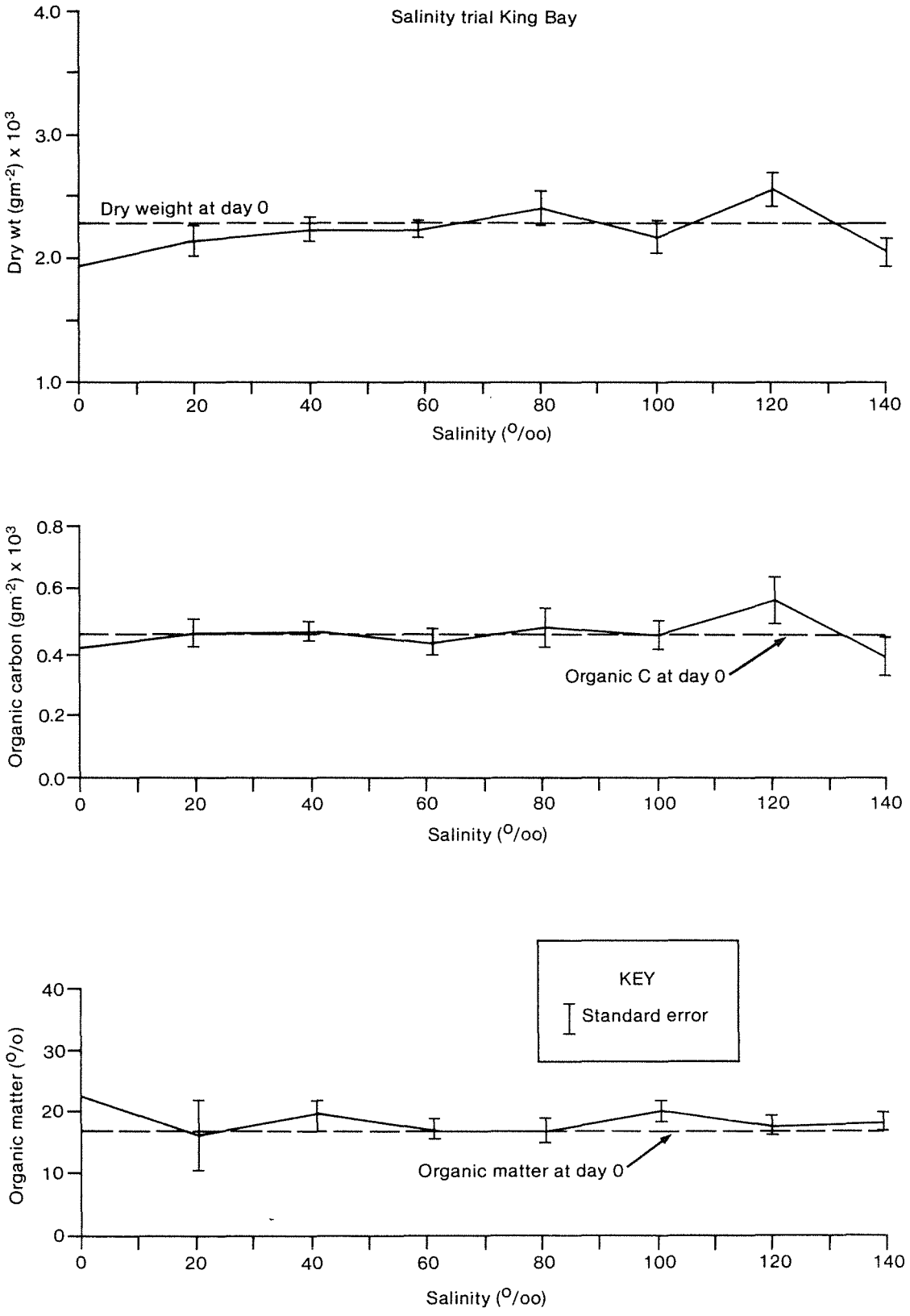


Figure 4.10 Dry weight, organic carbon and % organic matter of algal mats from King Bay after 23 days under different salinities

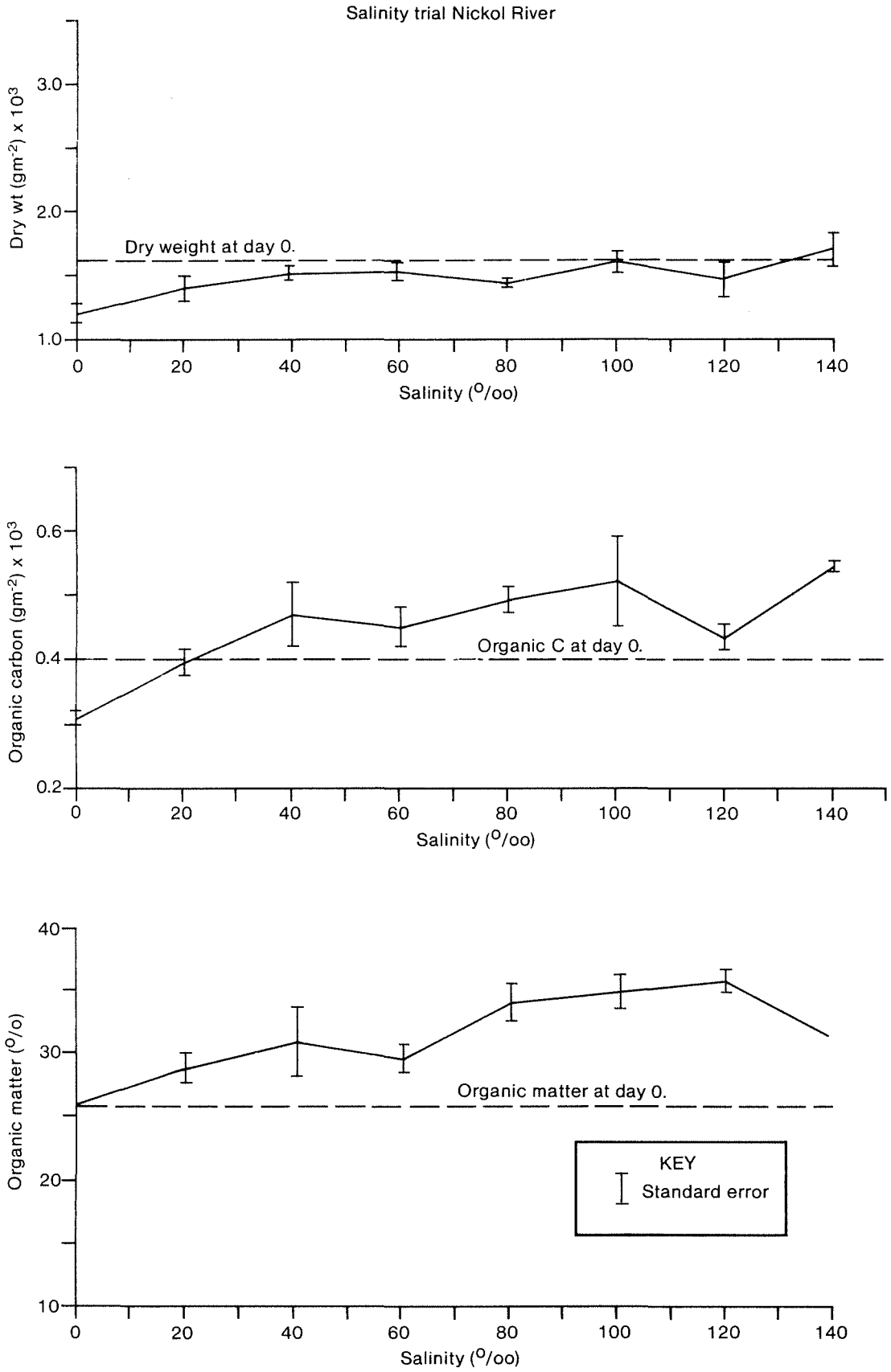


Figure 4.11 Dry weight, organic carbon and % organic matter of algal mats from Nickol River after 23 days under different salinities.

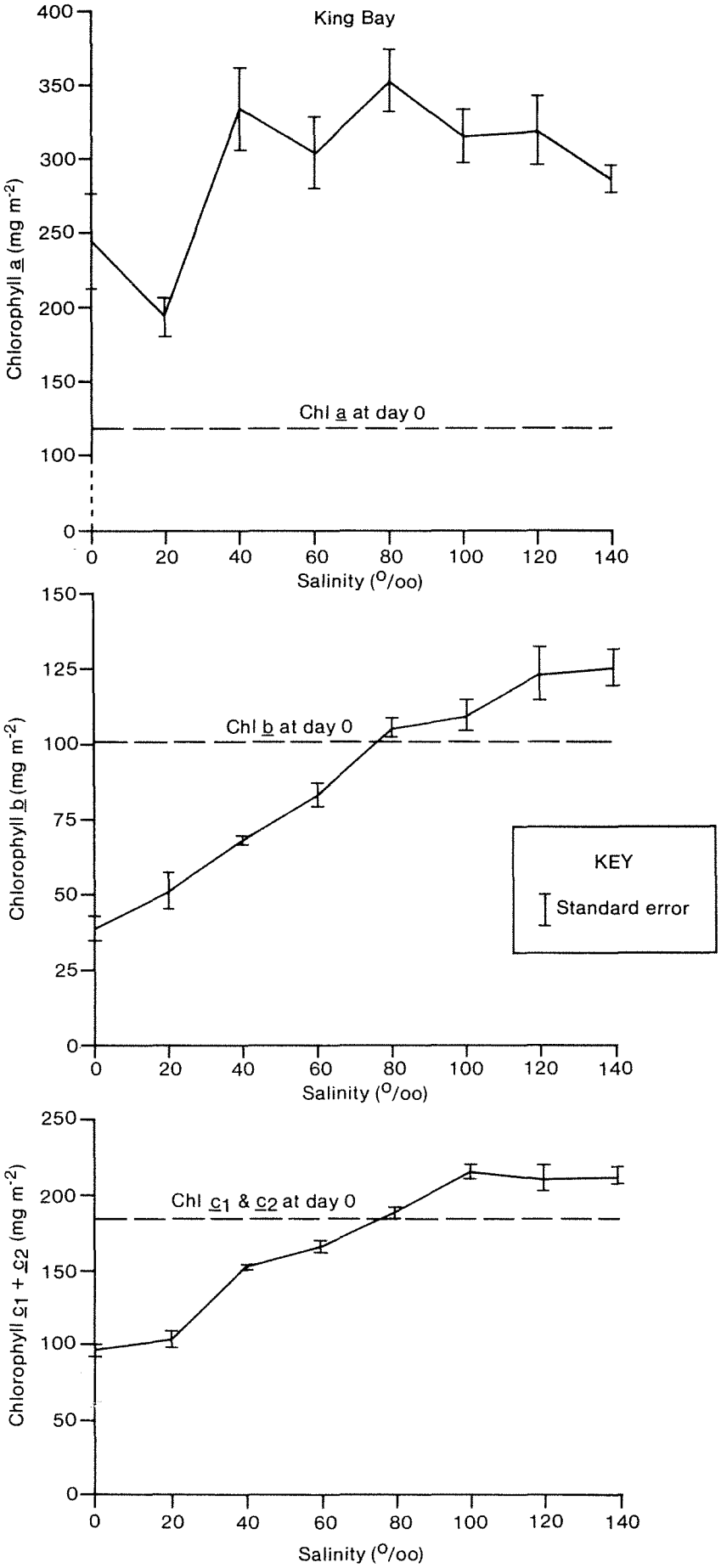


Figure 4.12 Chlorophyll a, b and $c_1 + c_2$ in King Bay algal mats after 23 days under a range of salinities.

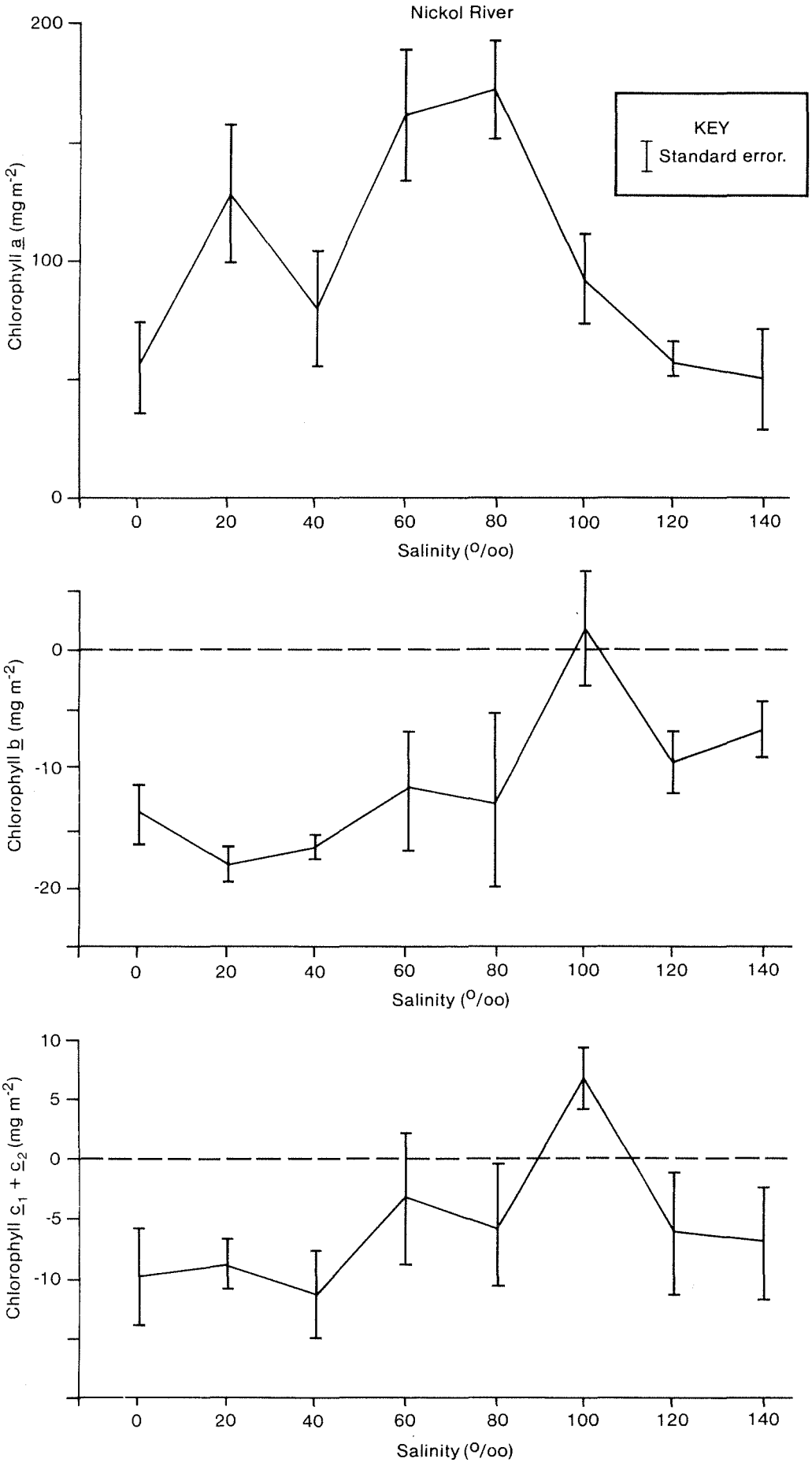


Figure 4.13 Chlorophyll a, b and $c_1 + c_2$ in Nickol River algal mats after 23 days under a range of salinities. Graphs show net increase or decrease from day 0.

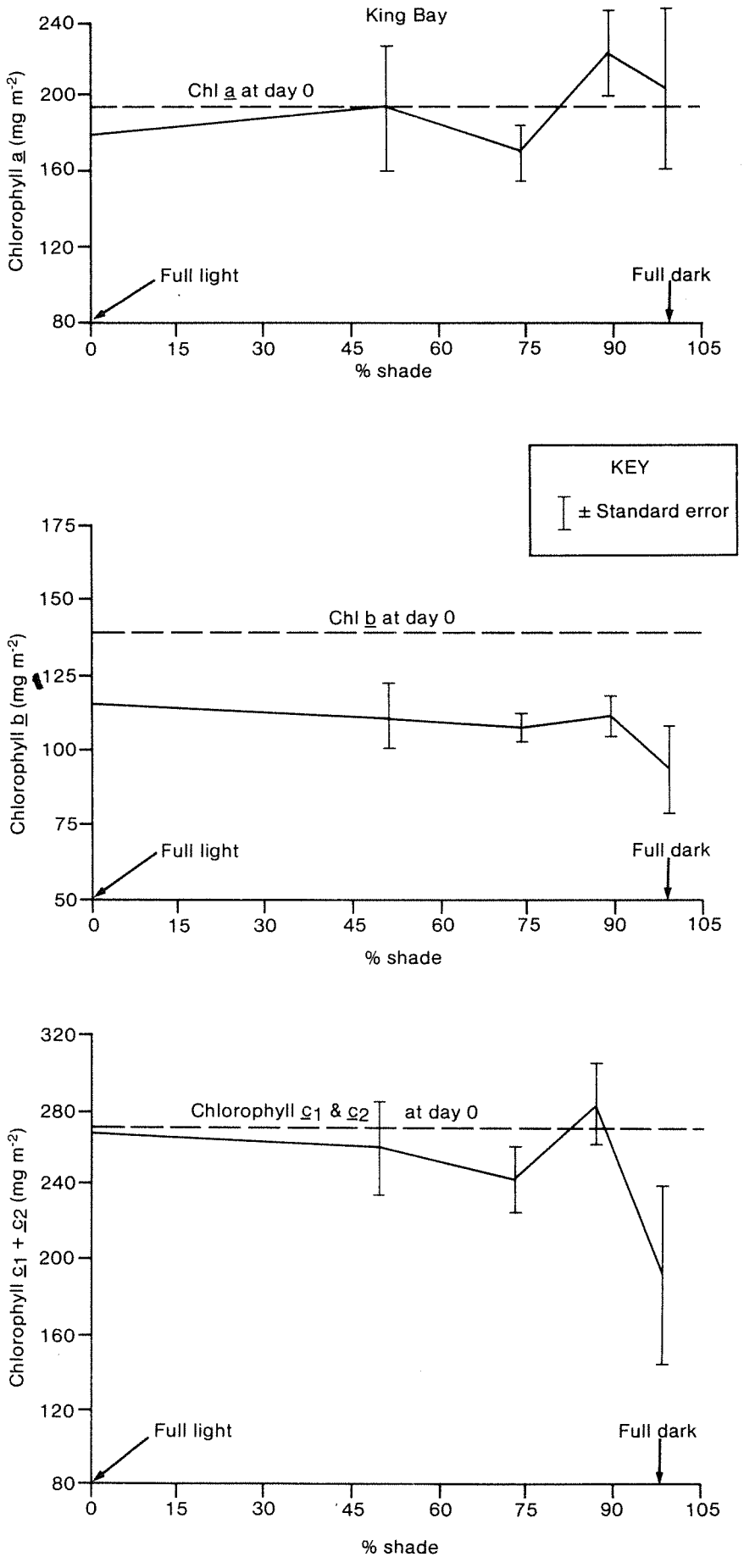


Figure 4.14 Chlorophyll a, b and c_1 + c_2 in algal mats after 42 days growth under a range of light conditions.

5. LEACHING AND TRANSPORT OF NUTRIENTS FROM ALGAL MATS

5.1 INTRODUCTION

The occurrence of nitrogen fixing cyanobacterial mats on pneumatophores and mangrove-associated sediments was well established by Potts (1979, 1980) in the Sinai Peninsula. Fixation in mangrove sediments has the potential to account for a large amount of nitrogen input into these systems (Table 5.1). The transfer of nitrogen from algal mats to coral reefs was illustrated by Burris (1976) and Goldner (1980), and to intertidal environments by Bohlool and Wiebe (1978).

Nitrogen that has been fixed, or stored, by cyanobacteria present in algal mats may become available in two main ways (Jones and Wilson, 1978):

(1) Organic nitrogen liberated from living cells to the outside environment during growth, and

(2) Nitrogen released on the death of cells.

The transfer of nitrogen and other nutrients from algal mats in terrestrial environments (Stewart, 1967; Mayland and McIntosh, 1966; Jones and Wilson, 1978) suggest that nutrient loss from mats could occur in an intertidal habitat, where they are periodically inundated by tide, exposed to freshwater runoff and washed by rainfall.

Two approaches were used to assess the potential of Dampier algal mats to supply nutrients by transport. The first was to measure the quantity of nutrients that could be leached from sections of mat in the field and the laboratory: the second to construct an enclosure in the field in which nutrient concentrations of a known volume of tidal water, passing over an algal mat, were examined over successive tidal cycles.

Table 5.1 Rates of nitrogen fixation in mangroves and mangrove-associated sediments.

Location	Association	Rate ($mg\ N\ m^{-2}d^{-1}$)	Annual input ($g\ N\ m^{-2}yr^{-1}$)	Study
Florida	sediment	7.8	-[1]	Zuberer & Silver, 1978
"	root	>>7.8	-	" "
Sinai	pneumatophores & mud	70.0	-	Potts, 1979
"	algal mats on sediment	219 - 2,010	-	"
"	pneumatophores & mud	28.9	-	Potts, 1980
"	"	6.0	-	"
Philippines	Avicennia[2]	2.4	0.86	Flordelis & Aspiras, 1981
"	Rhizophora[2]	2.2	0.79	"
"	Sonneratia[2]	2.1	0.77	"
"	Nypa[2]	1.1	0.41	"
Florida	Decomposing leaves	110 kg^{-1}(dry wt) d^{-1}	-	Gotto & Taylor, 1976

[1] Denotes not stated or not applicable (many are seasonal)

[2] Measurements taken in sediments below plants

Table 5.2 Nutrient fluxes in the enclosure at King Bay (July, 1983), figures are shown in mg m^{-2} of the 17 m^2 enclosure.

Date	Nutrient ($mg\ m^{-2}$)									
	NH_4-N		NO_3-N		PO_4-P		TN		TP	
	in	out	in	out	in	out	in	out	in	out
09.07.83	0.11	0.098	0.89	1.29	0.31	0.28	17.26	17.93	2.63	2.56
10.07.83	0.12	1.04	0.32	0.77	0.55	0.63	44.50	58.77	6.17	9.52
11.07.83	0.001	0.013	3.34	1.84	0.99	1.28	68.06	84.62	10.08	12.56
12.07.83	1.06	1.61	3.18	4.37	2.38	2.83	79.94	122.80	11.15	27.24
13.07.83	0.72	0.63	0.35	0.39	0.26	0.24	9.89	9.93	2.12	1.58

5.2 METHODS

Contouring of the study area

Contour maps of the King Bay area were prepared from elevation measurements made by the Karratha Lands and Survey Department.

The areas of algal mat cover in King Bay were calculated by planimetry using an electronic digitizer (Summagraphics Corp., Fairfield, Connecticut, U.S.A.).

Leaching experiments

Initially at King Bay (May, 1983), 300 x 150 mm plastic containers with their bases removed were pushed into the algal mat surface, ensuring a tight seal between the container sides and mat. Seawater was poured into these containers with the aim of sampling the water after a three hour period, but water flowed through the mat within ten minutes.

In May and July 1983, squares (80 x 80 mm) of mat were cut from the transects, and other areas, at King Bay (Figure 5.1) and Dampier Salt; placed in 500 ml containers in the field or the laboratory, and 300 ml of freshwater or saltwater added. Water samples were removed initially for analysis, and then at varying intervals, over a period of three hours. Two or four replicate samples were used for each analysis.

Similar methods were used to examine areas of algal mat from King Bay when dry, and after one tidal cycle. For comparison with the leaching characteristics of mats, 100 g samples of sediment beneath algal mat, and in adjacent non-mat covered areas were collected and treated as above.

Samples of dry, wet and friable mat at Dampier Salt were subjected to similar treatment. Water and algal mat samples were analysed using the same methods as those described in the following section for analysis of samples from the enclosure.

Enclosure

Construction. An enclosure 17 m (long) x 1 m (wide) x 1.3 m (high) was built at King Bay in July 1983 (Figure 5.1, Appendix Figure 1). Surveying poles were positioned vertically through the mat surface and the tops connected with surveyors string. Plastic sheeting (Gasden, 250 u thick, 2 m wide) was fastened to enclose a 17 x 1 m channel open at the seaward end. The bottom edge of the plastic was buried in sediment to 200 mm, with a tight seal between the plastic and the algal mat within the enclosure. Two, 120 mm wide open-ended, perspex tubes were fitted vertically into the algal mat at the enclosure entrance for sampling purposes and a tape measure fixed to an exterior pole to measure depth.

The height of the water was measured at the entrance of the enclosure, and noted more frequently when the tidal water had reached the end of the enclosure. This was done to determine the slope of the substrate for volume calculations.

Sampling. Water samples were collected in prewashed one litre plastic bottles over five successive tidal cycles from the 9.7.83 to 13.7.83 inclusive (Figure 5.2). The algal mat in the enclosure was exposed (i.e not inundated by the tide) for seven days before the first tide on the 9.7.83. Over a given tide cycle two replicates of eight to ten water samples were collected, divided equally between tidal rise and ebb. On 9.7.83, four replicates were taken at each sampling time. Efforts were made not to enter the water at any time during the tidal cycle.

Dissolved oxygen and temperature were measured with a Model 2110 multi-range analyser (Envirotech), and salinity at first with a Model 602 Temperature-Salinity bridge (Hamon), and from 10.7.83 onwards with a portable, temperature-compensated refractometer (American Optical Company, U.S.A.). The multi-range analyser and bridge temperatures were calibrated by taking simultaneous readings on each instrument ($r_{20} = 0.9750$, $p < 0.05$).

Sample analysis

Water samples collected from leaching experiments and the enclosure were treated and analysed as follows:

Samples for total nitrogen and phosphorus were poured directly into Whirl Paks (Nasco) and frozen. Samples for nitrate, ammonium and phosphate analysis were collected by the vacuum filtering of water through 47 mm diameter GFC filters (Whatman), stored in Whirl Paks and then frozen.

Water, sediment and mat samples were analysed for nutrient content and dry weight by the methods described in Chapter 4.

5.3 RESULTS

Nutrients leached from algal mats

A comparison between May and July indicated that, on a square metre basis, there were similar quantities of nutrients leached from mats on each occasion at King Bay and Dampier Salt. Very high nitrate concentrations were recovered in leachate after inundation with freshwater of King Bay mat samples collected in May. Nitrate contributed most to total nitrogen (100 - 400 mg NO_3-N g^{-1} algal mat). Ammonium, phosphate and total phosphorus were also leached, though in lower quantities (2 - 40 ug g^{-1} algal mat).

Conversely in July, organic nitrogen formed a major part (93%) of the total nitrogen leached from the mats by freshwater and seawater (10 - 30 mg m^{-2}).

Time course experiments conducted in July at King Bay indicated that all nutrients were leached from mats in added seawater within 60 minutes, with little further loss (Figure 5.3). The tapwater used for freshwater leaching studies already contained high nitrate concentrations (1.25 mg L^{-1}), and only ammonium leached into this water (Figure 5.3). All other nutrients were absorbed. Regardless of the process, most leaching or absorption occurred in freshwater in less than eight minutes, with little further change.

Algal mat and sediment from King Bay in July leached all nutrients, except phosphate, in freshwater (Figure 5.4). Sediment from beneath the mat and that present under bare soil broadly followed the same trends - more nutrients being leached into freshwater than into seawater, although greater losses usually occurred from sediment under the algal mat.

There were little differences in nutrient leakage, with the exception of total phosphorus (Figure 5.4), between mats from points 3 and 4 at King Bay. Losses from mats growing by the samphire zone were generally low.

Seawater leached all nutrients from mats at Dampier Salt collected in July (Figure 5.5); friable mat losing larger quantities. Freshwater caused loss from mats of all nutrients except phosphate.

The nitrogen and phosphorus content of all algal mats from King Bay remained constant at 1.57 - 2.08 mg g^{-1} and 0.21 - 0.26 mg g^{-1} respectively (N:P = 7-8:1) in May and July. This changed little or not at all before and after

inundation. Similarly, no notable changes occurred in Dampier Salt mats which maintained an N:P ratio of 7:1.

The predicted tidal inundation of algal mat over one year in King Bay

The King Bay site was covered by approximately 0.510 ha of algal mat, and 0.486 ha of this is covered on a 3.9 m tide (corresponding to the 1.4 m contour in Figure 5.1). None of the mat is inundated on a 3.8 m tide, and a 4.0 m (or higher) tide covers the total mat area. The inundation of algal mat in King Bay was derived from tide predictions for 1983 (Australian National Tide Tables, 1983). Predicted tides were used because of the difficulty in measuring actual tide levels. The difference between predicted and actual tides was as great as 500 mm (Figure 5.6), but the overall coverage, in regard to the days inundated, remained essentially similar for predicted and actual tidal inundation.

The algal mat in King Bay would be immersed on approximately 245 days of the year (67%) and this would usually be twice a day for two to three hours. The longest period the lower algal mat (the 1.4 m contour and below on Figure 5.1) was exposed was seven days, but on average five days. The seven day exposure period in 1983 occurred in winter.

Another characteristic of tidal inundation in King Bay was the time taken to flood and ebb; tidal water took longer to ebb than it did to flood. This was caused by a shallow water effect that gave rise to an asymmetrical tidal wave (Komar, 1976), which reduced the period of flood (tidal rise) and increased the time of tidal ebb. This may have had profound effects on the amount of nutrients leached from algal mats because the overlying water was essentially outgoing for a longer period of time. The asymmetry of tidal

currents has been shown to be important in exporting plant litter in mangrove creeks (Wolanski et al., 1980).

Volume and nutrient flux in the King Bay enclosure

Sampling was undertaken over five tidal cycles from the 9th to 13th July 1983 inclusive. The tide on the 13th July occurred at night. The methods for estimating volume change within the enclosure and the generation of the volume curves for each tidal cycle are given in Appendix 2.

Instantaneous flow rates were calculated by taking the volume change over a measured time interval. These rates were then used to calculate mass nutrient, salinity and oxygen flux (Appendix 2).

An example of the method of calculation for mass nutrient flow is given in Appendix 2, using data for NH_4-N.

Nutrient fluxes in the enclosure are presented in Table 5.2, and net gains and losses in Table 5.3. The values in Table 5.3 marked with an asterisk are those that have estimates of errors exceeding the net value. These errors preclude stating, with any certainty, whether they have been imported or exported. Significant export therefore took place of ammonium, organic nitrogen and organic phosphorus.

Inorganic nutrient concentrations in tidal water entering and leaving the enclosure were generally low, the ranges being: NH_4-N (2 - 18 ug L^{-1}), NO_3-N (0 - 30 ug L^{-1}) and PO_4-P (1 - 7 ug L^{-1}). Total nitrogen (Figure 5.7) and total phosphorus were present in high concentrations, but there were large variations in total phosphorus values (Figure 5.8) over all tidal cycles sampled.

Table 5.3 Net gains (+ ve) and losses (- ve) from algal mat in the King Bay enclosure.

Date	Nutrient (mg m^{-2})					
	NH_4-N	NO_3-N	Organic N	PO_4-P	TN	TP
09.07.83	+0.012 *	-0.40 *	-0.28	+0.03 *	-0.67	+0.07
10.07.83	-0.92	-0.45	-12.90	+0.08 *	-14.27	-3.35
11.07.83	-0.011	+1.50 *	-18.05	-0.29 *	-16.56	-2.48
12.07.83	-0.55	-1.19	-41.12	-0.45 *	-42.86	-16.09
13.07.83	+0.09	-0.04	-0.09 *	+0.02	-0.04 *	+0.54
Totals	-1.38	-0.58 *	-72.44	-0.77 *	-74.40	-21.31

* Error terms exceed net value: thus significant changes cannot be predicted.

Table 5.4 Predicted nutrient fluxes in King Bay derived from the experimental enclosure used in this study. Totals represent the net flow of nutrients over five successive tidal cycles.

DATE	TIDE HEIGHT	ALGAL MAT AREA (ha)#	NUTRIENT FLOW (grams)														
			NH_4-N			NO_3-N			PO_4-P			TN			TP		
			IN	OUT	NET *	IN	OUT	NET	IN	OUT	NET	IN	OUT	NET	IN	OUT	NET
09.07.83	3.9	0.486	0.573	0.505	+0.068	4.824	6.985	-2.161	1.624	1.440	+0.184	89.113	92.594	-3.481	13.609	13.222	+0.387
10.07.83	4.2	0.510	0.515	5.643	-5.128	1.743	4.204	-2.461	3.167	3.424	-0.257	123.880	318.493	-194.613	33.447	51.606	-18.159
11.07.83	4.4	0.510	0.011	0.024	-0.013	18.086	9.960	+8.126	5.379	6.958	-1.579	329.515	458.746	-129.231	54.662	67.760	-13.098
12.07.83	4.5	0.510	5.737	8.719	-2.982	17.212	23.693	-6.481	12.909	15.346	-2.437	433.181	663.045	-129.864	63.591	147.619	-84.023
13.07.83	3.9	0.486	3.709	3.244	+0.465	1.833	1.998	-0.165	1.357	1.242	+0.115	51.050	51.291	-0.241	10.968	8.168	+2.782
Totals					-7.59			-3.14			-3.97			-557.43			-112.12

* "+" Denotes net import of nutrient
"-" Denotes net export of nutrient

\# covered by tide

Nutrient flux estimates for the entire King Bay algal mat

These were calculated over the five tidal cycles for the King Bay system as follows:

Area of algal mat in enclosure = 16 m^2

Area of algal mat covered on 9.7.83 and 13.7.83 (3.9 m tide) = 0.486 ha.

Area of algal mat covered on 10.7.83 - 12.7.83 (> 3.9 m tide) = 0.510 ha.

Total nutrient flow in/out of King Bay over 5 tidal cycles = (Area of algal mat covered (m^2)) X (Nutrient flux from enclosure) ($16\ m^2$).

These figures are shown in Table 5.4.

When estimates are made for five tidal cycles from the enclosure and extrapolated for the entire algal mat at King Bay, there was a net loss of all nutrients (Table 5.4). The inorganic nutrient losses were generally low, and were variable on each tidal cycle. Only total nitrogen showed a net loss over all cycles. Organic nitrogen and organic phosphorus showed high losses.

Salinity and temperature changes in the enclosure

The water entering the enclosure on the first tide (9.7.83) had a high salinity, 47 $^{o}/_{oo}$ and left at 60 $^{o}/_{oo}$ (Figure 5.9). There was less salinity increase on the second tide, and little change after this. If similar evaporation rates are assumed, the higher salinity on the first day must have been derived from the algal mat. Alternatively, the higher temperature recorded on 9.7.83 (Figure 5.10) may have contributed to higher evaporation rates and thus higher salinities.

On the first two tidal cycles there was a net loss of approximately 67 kg of salt from the enclosure (Table 5.5). On the third tide there was a net gain, and thereafter there were only minor losses or gains. For comparison, the amount of salt contained within the enclosure when the water depth was 0.5 m was 334.7 kg (ie. 20 kg m^{-2}) for seawater of 35 $^{o}/_{oo}$.

Water temperatures were higher on the ebb tide (Figure 5.10). The greatest difference in water temperature between flood and ebb tides was recorded, as for salinity, on the first tide to inundate the mat.

Oxygen flux

The oxygen content of water in the enclosure increased on outgoing tides (Figure 5.11). On all tidal cycles examined there was a net loss of oxygen to water leaving the enclosure (Table 5.6, Figure 5.11). By calculating the amount of oxygen lost from the algal mat over each tidal period, it was seen that the activity of the mat when immersed progressively increased from 0.5 g m^{-2} hr^{-1} on the first tide to 4.6 g m^{-2} hr^{-1} on the third.

5.4 DISCUSSION

Nutrients

Organic nitrogen was the predominant form of nitrogen lost from the enclosure on the tidal cycles sampled, values ranging from 0.28 - 41.12 mg N m^{-2} (Table 5.3). Data from the leaching trials support this; levels of organic nitrogen (8 - 22 mg N m^{-2}) were lost from algal mats immersed in seawater in July (Figure 5.3, 5.4).

Jones and Wilson (1978) suggest that organic nitrogen may be liberated from living cyanobacterial cells to the environment during growth. As July was in the period when the mat was growing well and most stresses were minimal

Table 5.5 The salinity flux in the enclosure at King Bay over five tidal cycles (see also Figure 5.9).

Date	In (+ ve) (kg)	Out (- ve) (kg)	Net (kg)*
09.07.83	42.158	83.850	-41.692
10.07.83	136.189	161.967	-25.778
11.07.83	268.253	215.857	+52.396
12.07.83	294.663	295.082	-0.419
13.07.83	31.644	24.186	+7.458

* Negative values show export and positive values import.

Table 5.6 The oxygen flux in the enclosure at King Bay over three tidal cycles (see also Figure 5.10).

Date	In (+ ve) (g)	Out (- ve) (g)	Net (g)	Activity+	
				Time mat immersed (min)	mg $m^{-2} hr^{-1}$
09.07.83	3.192	7.815	-4.623	103	493.6
10.07.83	11.564	23.581	-12.017	173	2159.3
11.07.83	6.225	29.921	-23.666	185	4560.6

* Negative net values show export.

\+ Activity per square metre was calculated from the 16 m^2 of algal mat contained within the enclosure.

(Chapter 3), it is possible that organic nitrogen may have been released at this time. This theory is supported by estimates of total nitrogen to total phosphorus ratios. At King Bay the ratio, which was derived from water from the enclosure, was 5:1 (Table 5.3). Furthermore, water from algal mat leaching experiments was 7:1 (Figure 5.3, 5.4) and the algal mat itself was 7 - 8:1.

These authors also suggest that cyanobacterial nitrogen can be released on the death of cells. Organic nitrogen dominated the total nitrogen content leached from algal mats in July (Figure 5.4). In May, however, nitrate formed a large proportion of the nitrogen lost. This discrepancy may represent seasonal changes in algal mat growth, growth occurred during winter (July) when leaching of particulate organic nitrogen took place, whereas, after summer (May), degradation and mineralization was accompanied by high nitrate losses.

From the data presented here annual nutrient losses from the King Bay system can be estimated. Annually, King Bay is inundated by approximately 310 tidal cycles, which would produce a loss of 34 kg of nitrogen a year (68 $kg\ ha^{-1}\ yr^{-1}$). The total nitrogen content in the algal mat at King Bay is estimated at 70 kg (Chapter 4). It is possible that the algal mat turnover and nitrogen fixation is sufficient to replenish this loss. Phosphorus losses are more difficult to determine, but data from the leaching trials suggest that the N:P ratio in leachate would be 5 - 8 N: 1 P. On a yearly basis this would suggest a loss of 7 kg of P, and for losses to occur from algal mats there would need to be some phosphorus input to the system. This input could stem from particulate material contained in seawater or from terrestrial sources. There is evidence that algal mats or sediment may absorb nutrients, particularly nitrate from freshwater (Figure 5.3).

Studies on tidal flats, flooded soils and mangrove-associated sediments have shown that fluctuating hydrologic regimes causing alternate aerobic and anaerobic conditions, lead to losses of nitrogen (Reddy and Patrick, 1975; Flordelis and Aspiras, 1981; Boto, 1982; Pedrazzini, 1983). Not all of the area covered by the tide in King Bay is algal mat, and thus leaching may occur from bare sediment (Figure 5.4), although on lower tides, there is more algal mat covered than bare sediment. An additional variation in algal mat nutrient loss would depend on the position of the algal mat on the mudflat. Different areas of King Bay are likely to leach varying quantities of nutrients. Nutrient loss, for example, is lower at a distance from the tidal creek and almost absent around the samphire zone (Figure 5.4).

Only five tidal cycles were measured in this study. Without further research, it is not possible to state whether these are representative of the whole year or even a bimonthly cycle. It may be that the initial inundation of the algal mat after a dry period is a critical period for nutrient loss; the mat may lose nutrients on the first few cycles, but regain integrity and biological activity, and lose little after this.

Algal mats at Dampier Salt had the same general leaching characteristics of those at King Bay (Figure 5.5). Little can be determined about nutrient transport, however, as this site has a different hydrological regime. Unlike King Bay, tidal water at Dampier Salt may remain for long periods of time over the algal mat (Chapters 2 and 4). The probable influence of leaching and its effect on algal mat growth in this system is discussed in Chapter 7.

Rainfall

Data which shows that freshwater has the potential to leach a large amount of nitrate from algal mats, particularly in May, and the rapidity of this response after immersion (Figure 5.3), suggests that significant nutrient losses may occur after rainfall. This is supported by two observations from King Bay: water readily flowed through the mat, and ponded water after rainfall rapidly disappeared and seeped into the adjacent tidal creek (A. Chiffings pers. comm.).

Salinity

The high salinities recorded in seawater on the first tidal cycle in King Bay (Figure 5.9) are likely to have resulted from two processes: firstly water passing through the mangrove creeks after a dry period may have absorbed salt before flooding the mudflat, and secondly salt crystallized on the mat surface over the dry period would have contributed to high salinities on the ebb tide. This is supported by the export of salt from the enclosure on the first two tidal cycles (Table 5.5). The input of salt to the enclosure on the 11.7.83 (Table 5.5) corresponds to a time when incoming seawater was initially high in salt content (Figure 5.9). The progressive decrease of salinities towards marine levels (Figure 5.9), and the minor losses and gains after the first three tides to cover the mat (Table 5.5), suggests some flushing of salt from the mudflat area. This may be important when considering the physiological restraints of salinity on algal mat growth at different times of the year.

Temperature

An increase in the temperature of the water on the mudflat area (Figure 5.10) was expected, as there was a large area covered by water of shallow depth. Higher tides, causing greater water depths, would be expected to

change less in temperature than lower tides. The progressive decrease in water temperatures over the days sampled may have been caused by wind-driven evaporation. Increases in water temperature are likely to be important to algal mat physiology, particularly on low summer tides, when water temperature is high.

Oxygen

Increased oxygen levels in water that had covered the algal mat (Figure 5.11), and the increase in exported oxygen levels and activity of the mat suggest not only that the algal mat was photosynthetically active, but that this activity increased with progressive immersion. This also suggests that there was an element of 'recovery' of the algal mat after a dry period. The rapid formation of oxygen bubbles on the mat after immersion (Chapter 3) supports this.

5.5 SUMMARY

- Experimental evidence is presented to show that algal mats lose nutrients, particularly nitrogen, when inundated by the tide after a dry period.
- In July, this nitrogen was lost in organic form and was probably derived from growing cyanobacterial cells. In May nitrate made up a high proportion of the nitrogen lost.
- The loss of nitrogen from algal mats was estimated to be equivalent to approximately half of the total nitrogen present in the biomass. A loss of phosphorus also occurred.
- It is speculated that nitrogen losses may be replenished by N_2-fixation, but phosphorus losses must be replenished by some outside source such as seawater and terrestrial sources.

- Freshwater leached large quantities of nutrients from algal mats in a short period of time. Thus rainfall, which flows readily through the mat and into adjacent tidal creeks, also has the potential to leach nutrients.
- Increases in temperature, salinity and oxygen levels occurred in tidal water resident on the algal mat. Temperature changes were probably caused by heating in the shallow water column; salinity by salt crystallized on the mat during the previous dry period, and oxygen by cyanobacterial photosynthetic activity.
- Algal mat productivity, as measured by water oxygen levels, was observed to increase progressively from 0.5 g m^{-2} hr^{-1} on the first tidal cycle to 4.6 g m^{-2} hr^{-1} on the third; this may be important when considering nutrient fluxes because as algal mat activity increases so would requirements for nutrients.
- Algal mats from Dampier Salt had similar leaching capabilities to those of King Bay, but the system in general possessed a different hydrologic regime, which would modify leaching characteristics.

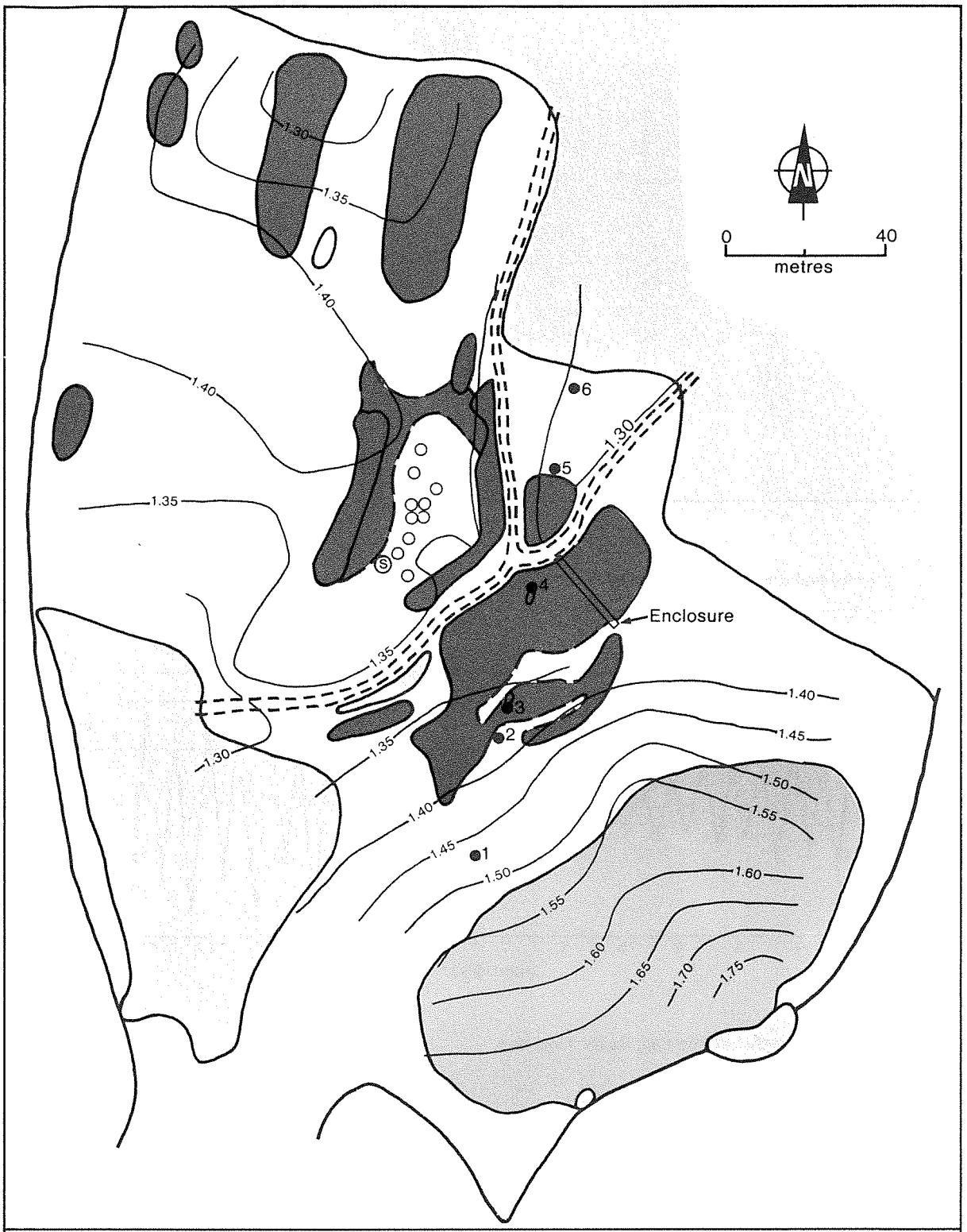


Figure 5.1 The King Bay study site showing the locations of the enclosure and points used for leaching experiments.

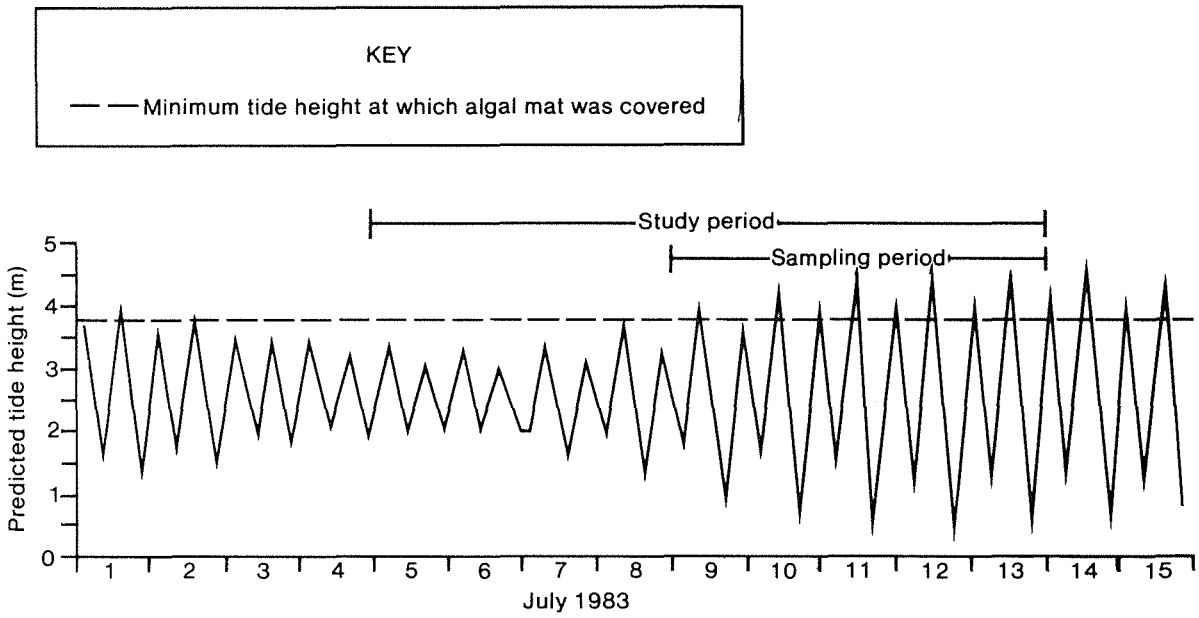


Figure 5.2 Predicted tide heights for King Bay.

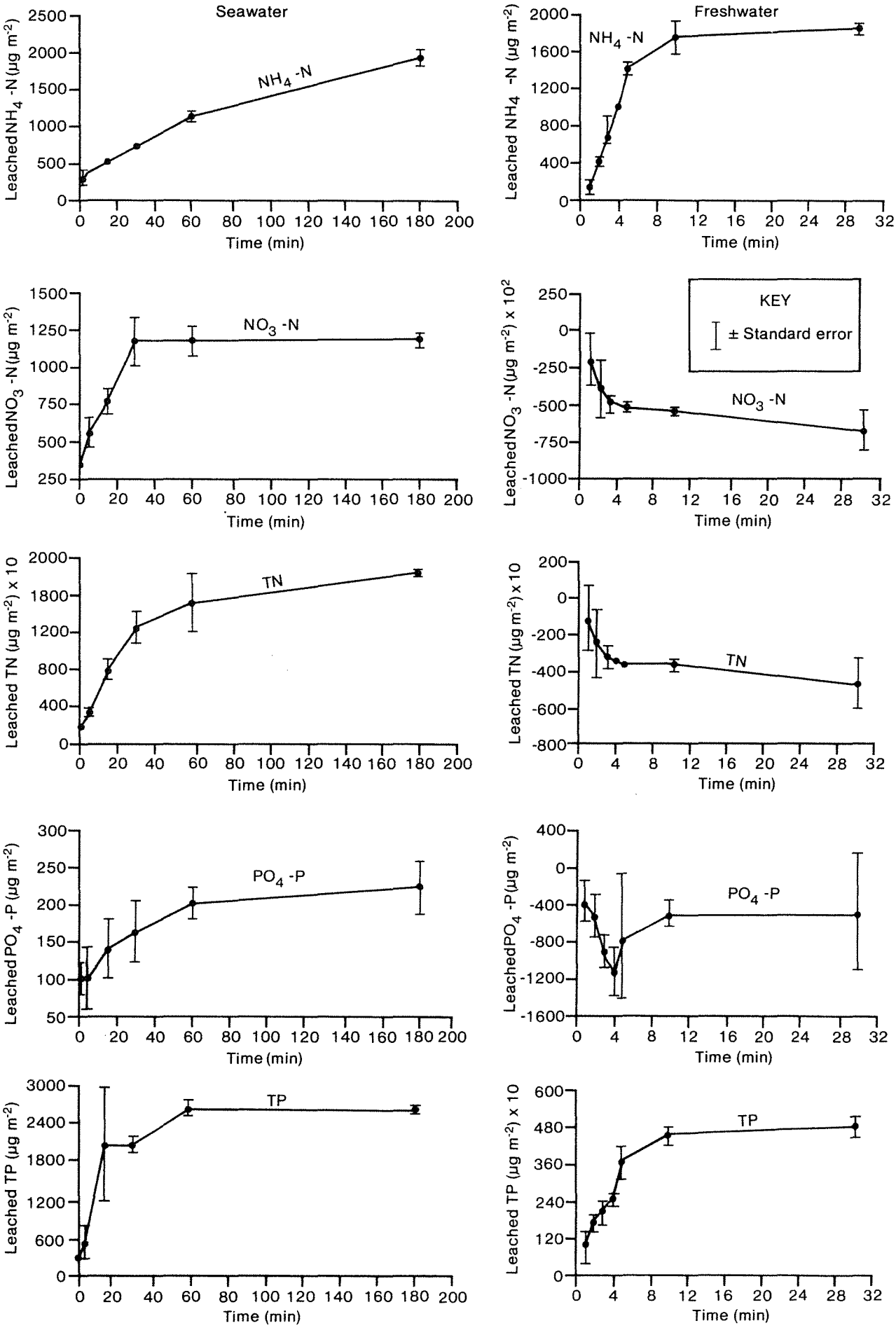


Figure 5.3 Cumulative leaching of nutrients from algal mats of King Bay into added seawater and freshwater containing nitrate.

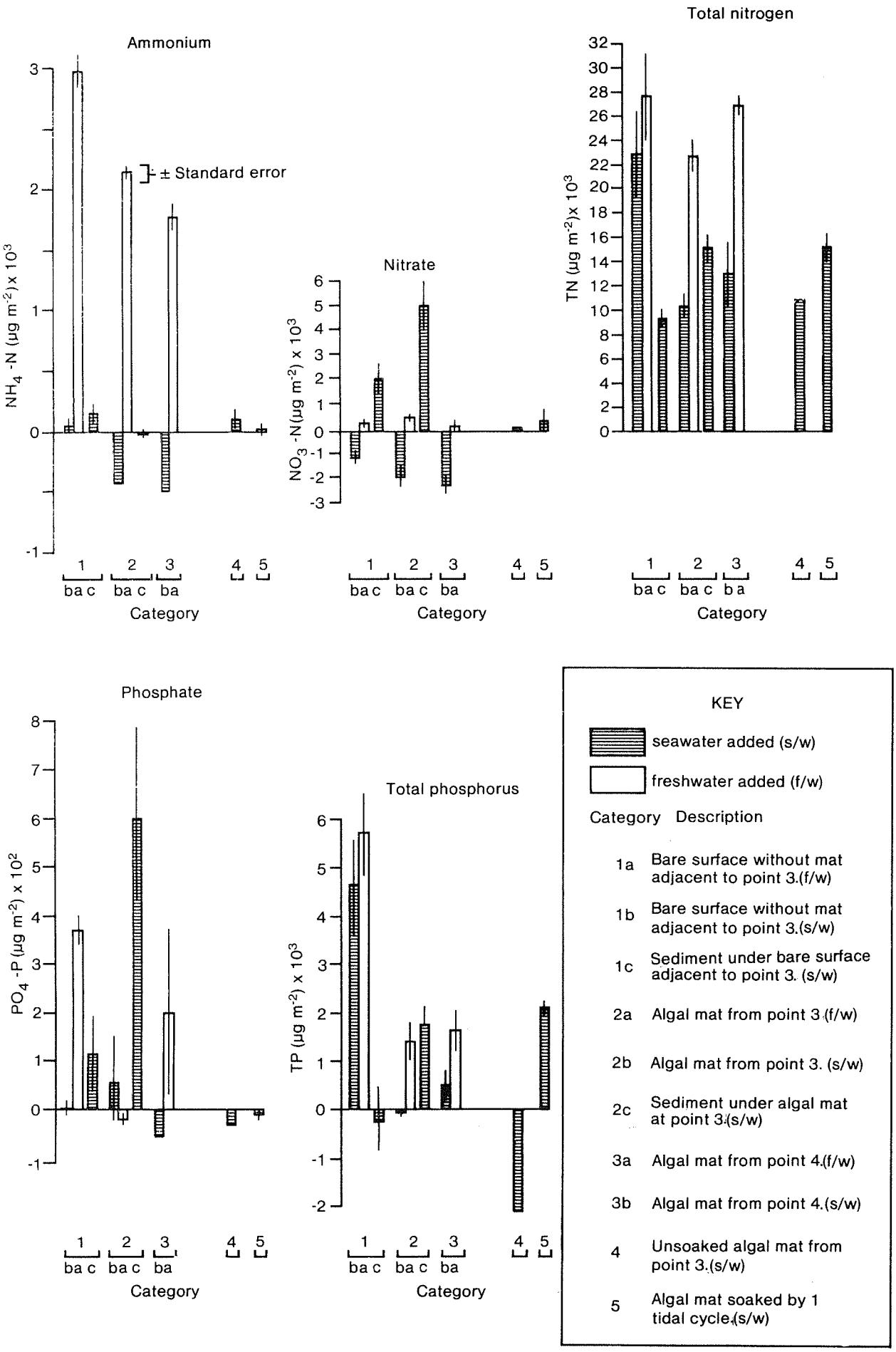


Figure 5.4 The loss (+ve) or gain (–ve) of nutrients from or to algal mat and sediment samples collected from different points at King Bay in July 1983, during inundation trials.

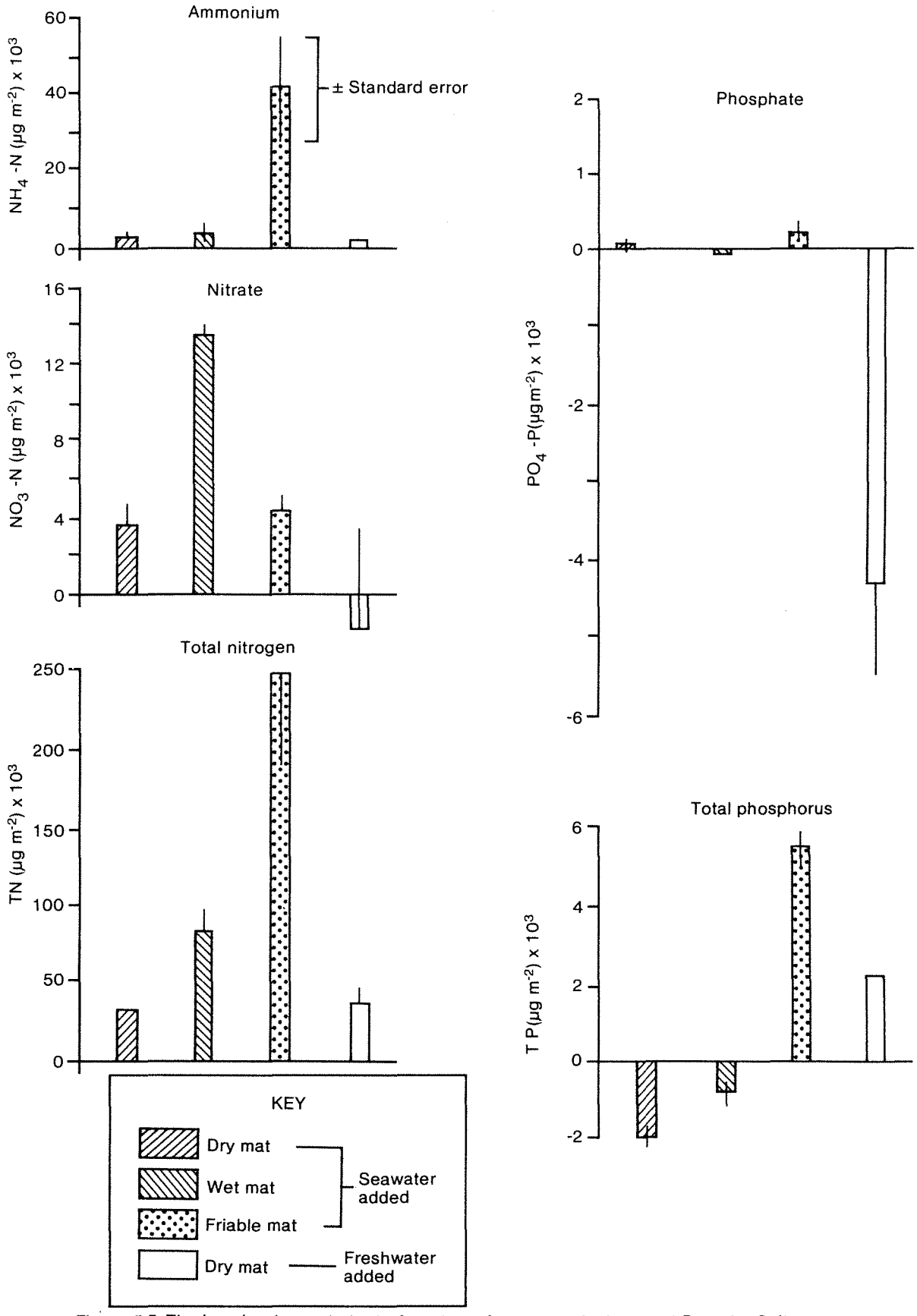


Figure 5.5 The loss (+ve) or gain (-ve) of nutrients from or to algal mats at Dampier Salt.

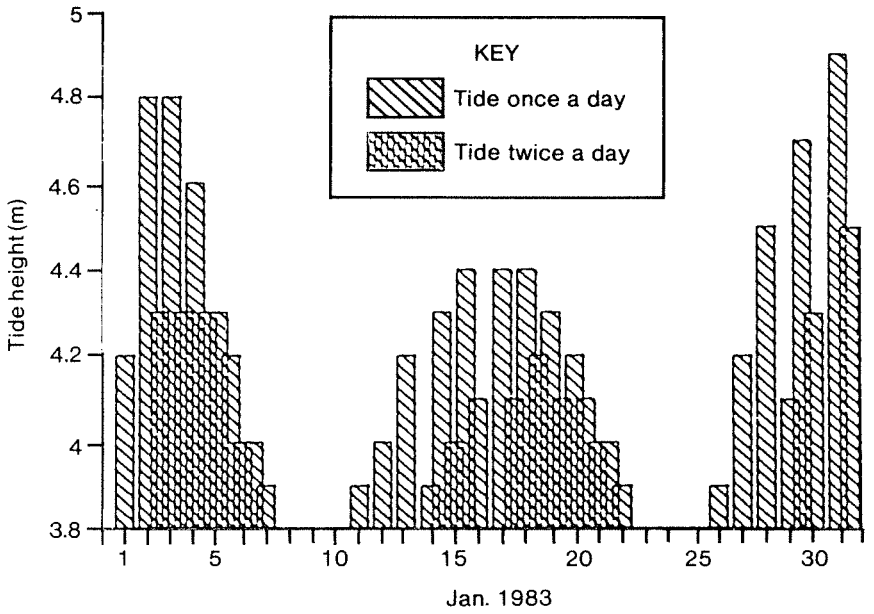


Figure 5.6a Frequency of inundation of algal mat by tide; King Bay, January 1983.

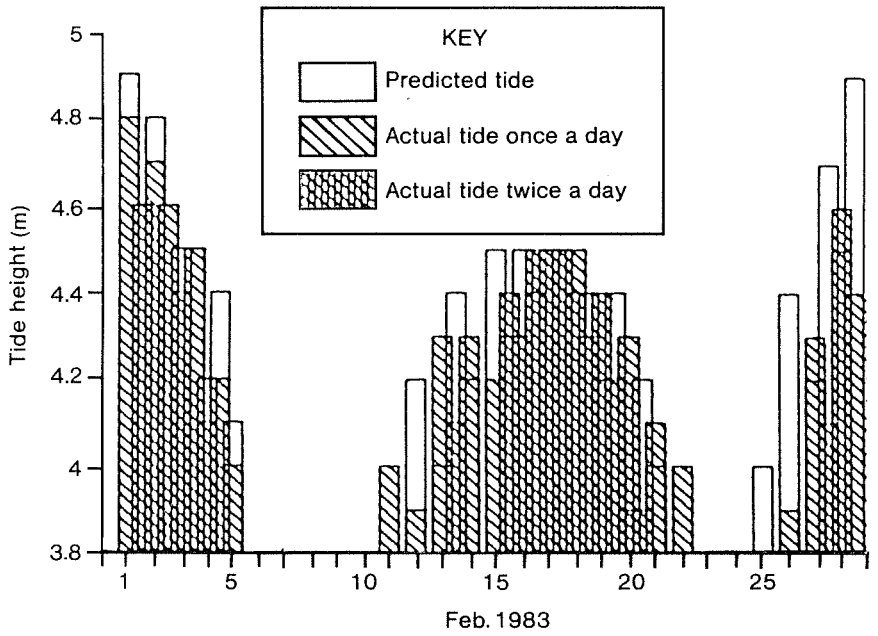


Figure 5.6b Frequency of inundation of algal mat by tide; King Bay, February 1983.

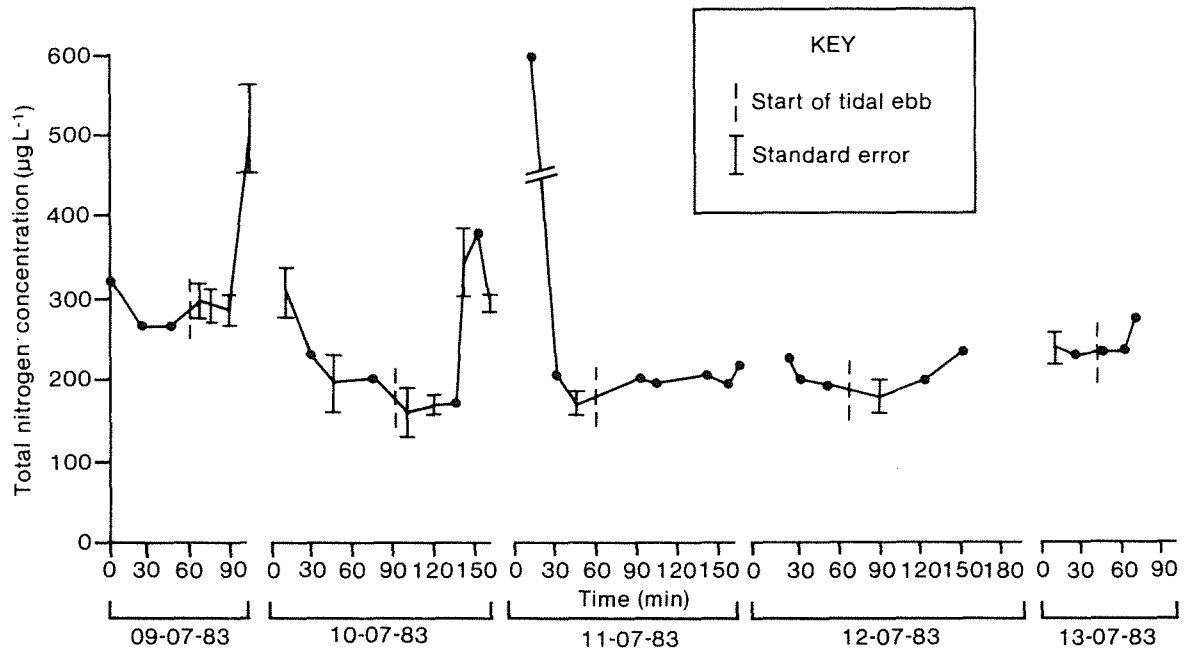


Figure 5.7 Concentration of total nitrogen in tidal water moving in and out of the enclosure at King Bay.

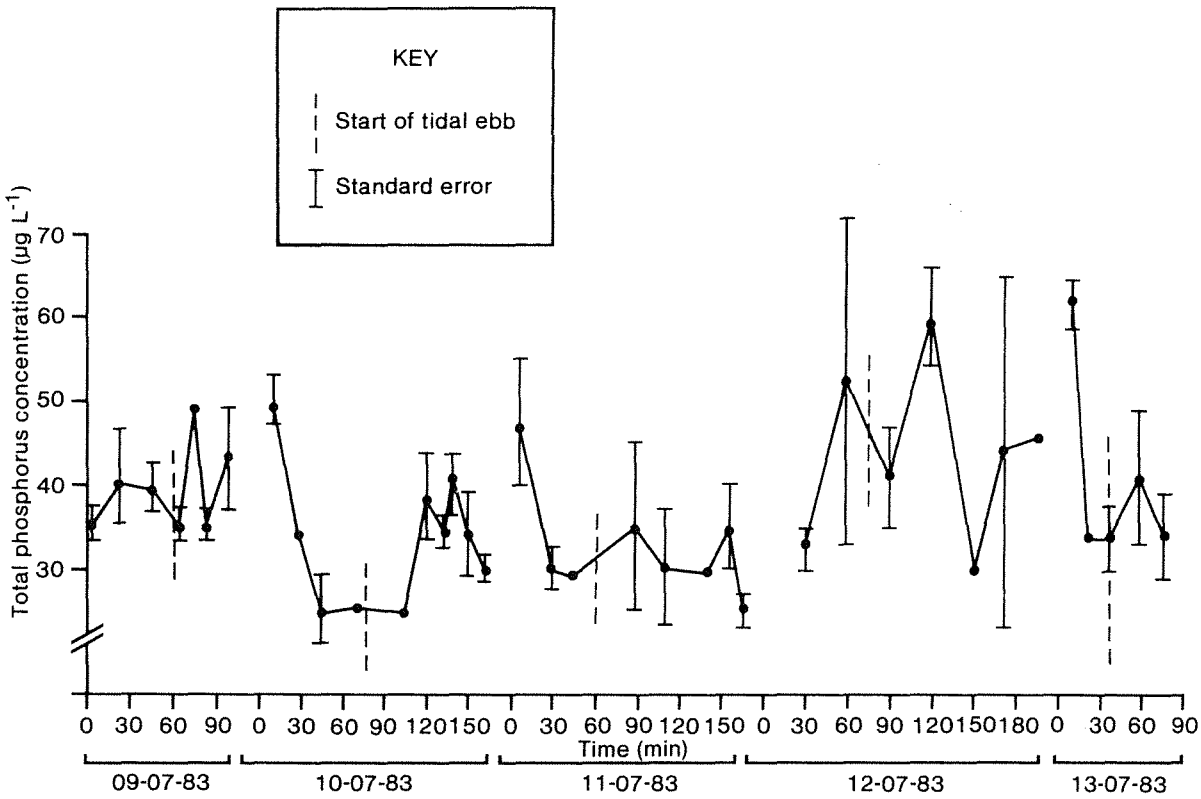


Figure 5.8 The concentration of total phosphorus in tidal water moving in and out of the enclosure at King Bay.

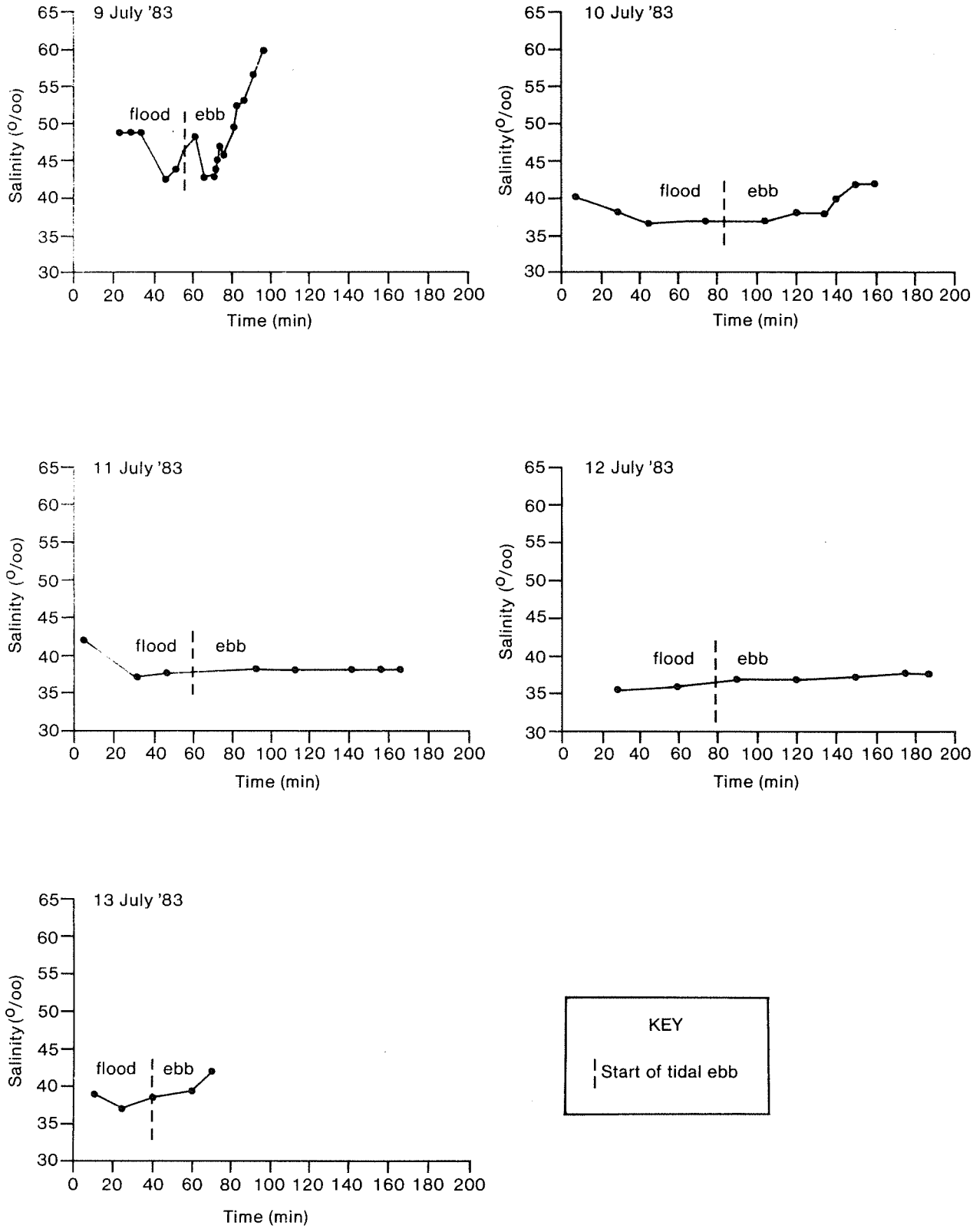


Figure 5.9 Salinity changes (°/oo) of tidal water over five tidal cycles in the King Bay enclosure.

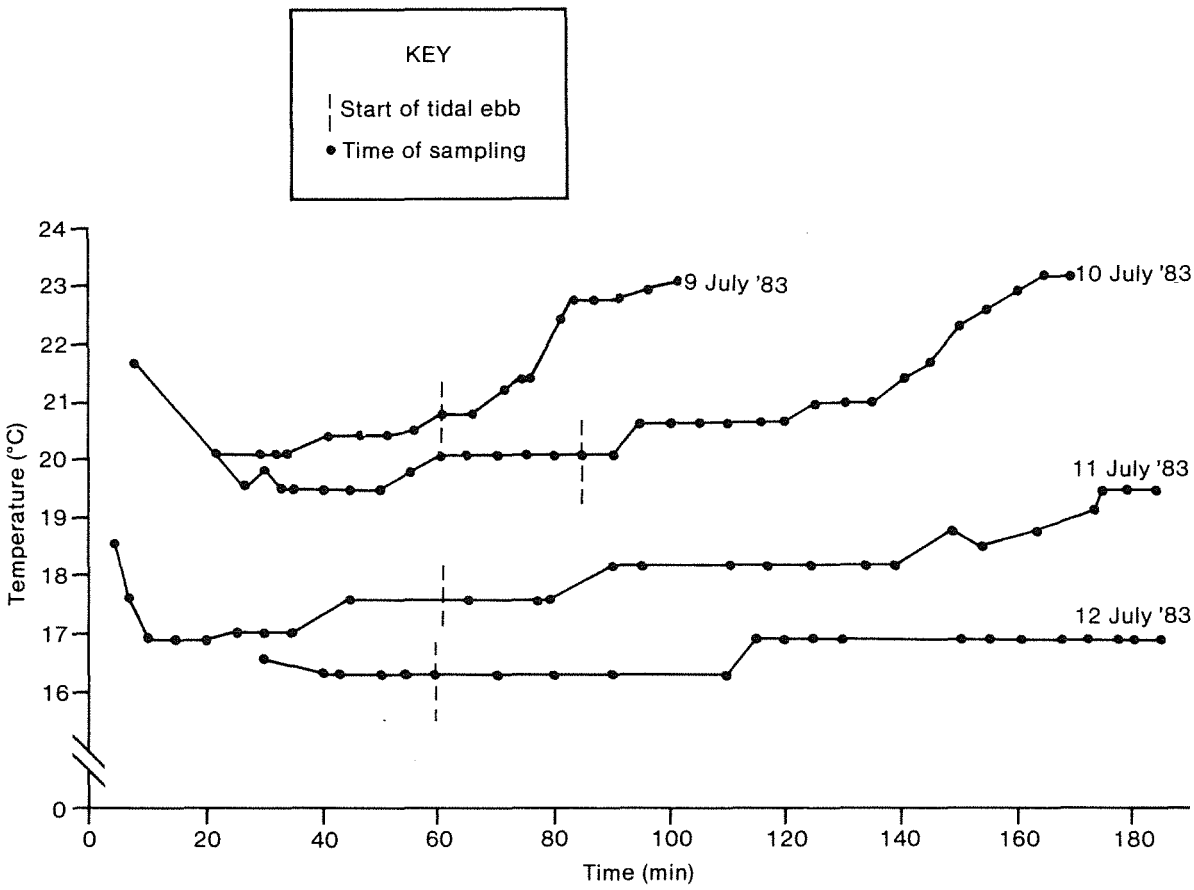


Figure 5.10 Temperature changes of tidal water moving in and out of the enclosure at King Bay.

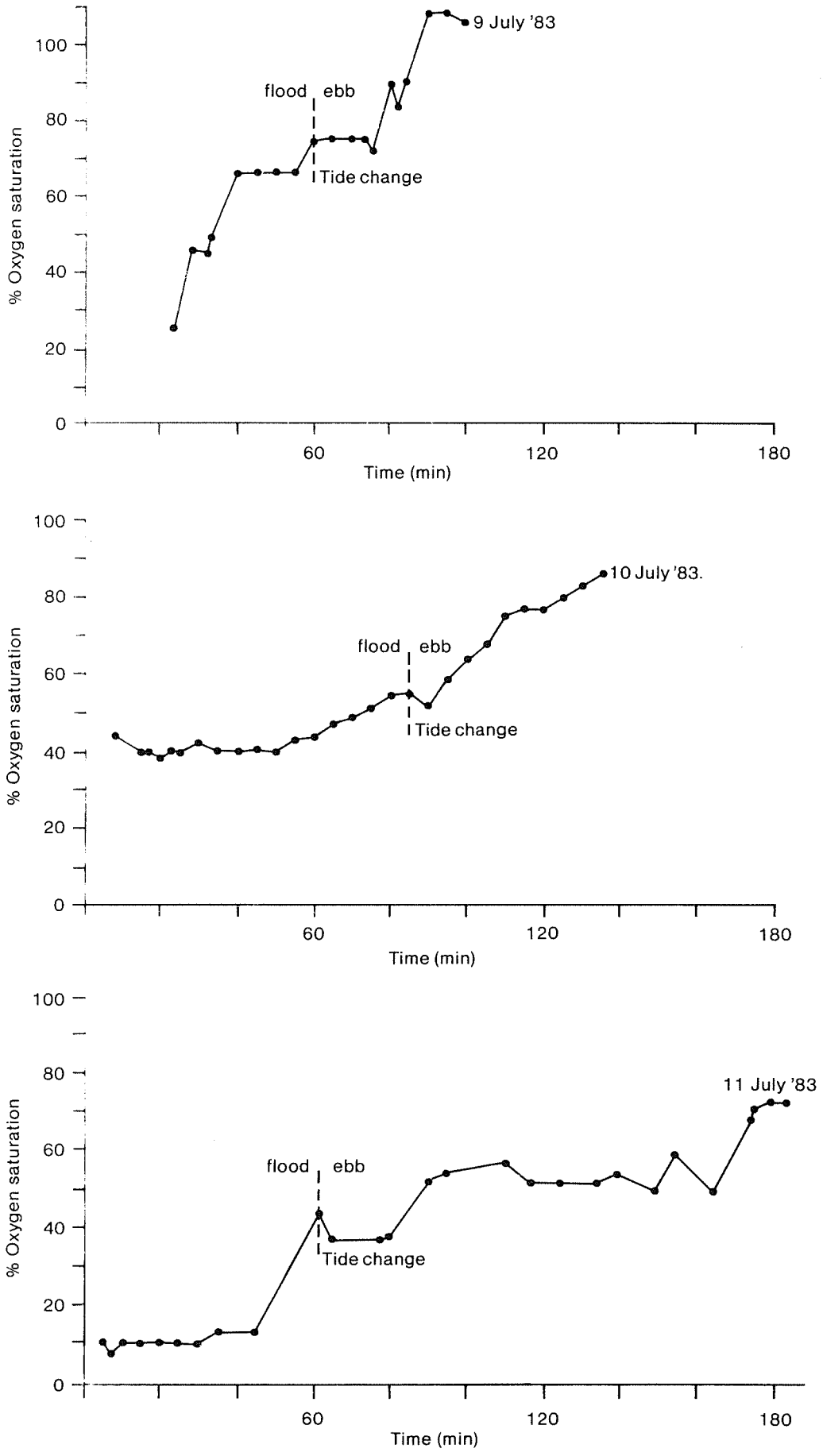


Figure 5.11 Oxygen saturation (°/o) of tidal water measured at the entrance of the enclosure at King Bay over three tidal cycles.

6. NITROGEN FIXATION IN DAMPIER ALGAL MATS

6.1 INTRODUCTION

This study was undertaken to examine the nitrogen fixing capabilities of Dampier algal mats, with regard to fixation rates. In addition, the effects of salinity, light and desiccation on this process were investigated to determine the environmental constraints on algal mat nitrogen fixation in the Dampier Archipelago. The available literature on factors affecting nitrogen fixation in algal mats is reviewed below.

In biological nitrogen fixation, atmospheric nitrogen is converted to ammonia by the action of the enzyme nitrogenase. This enzyme consists of two redox proteins in conjunction, both of which are rapidly and irreversibly inhibited by oxygen. For this reason, one of the overriding principles of the physiology of nitrogen fixation is the protection of nitrogenase from oxygen damage (Robson and Postgate, 1980). A particular problem for nitrogen fixing cyanobacteria is that they produce oxygen photosynthetically, through the photolysis of water. Oxygen can have three effects; it can cause a rapid inhibition of nitrogenase which can be reversed in the short-term; it can irreversibly inhibit the synthesis of nitrogenase polypeptide units; and finally oxygen can irreversibly inhibit existing nitrogenase (Stewart, 1980).

One cyanobacterial group has evolved a protective mechanism for nitrogenase, in the form of specialized cells termed heterocysts (Haselkorn, 1978). These lack the enzymes capable of photolysing water, and contain nitrogenase which is protected from oxygen. The nitrogenase catalyses nitrogen fixation using energy derived from neighbouring cells. There are many reports of free-living, heterocystic, nitrogen fixing cyanobacteria (Stewart, 1980; Stewart *et al.*, 1982), and also of fixation in algal mats containing these

organisms (Warmling, 1973; Jones, 1977c; Potts and Whitton, 1977; Finlayson and McComb, 1978; Potts, 1979; Wickstrom, 1980; Allnut et al., 1981; Reynaud and Roger, 1981). Carpenter and Price (1976), however, were among the first workers to demonstrate that a species of Oscillatoria, a non-heterocystic cyanobacterium, was able to fix nitrogen because it possessed reduced pigment levels in the central cells of a colony. These cells did not photosynthesize, and provided an oxygen-protective mechanism for nitrogenase. Recently other non-heterocystous cyanobacteria have been reported as able to fix nitrogen under low oxygen tensions (Kalininskya et al., 1981), and even under aerobic conditions (Saino and Hattori, 1982).

While there have been reports of totally non-heterocystous, cyanobacterial mats fixing nitrogen (Potts and Whitton, 1977; Potts, 1979; Allnut et al., 1981; Stal and Krumbein, 1981; Love et al., 1982; Stal et al., 1984), relatively few of the non-heterocystous species have been shown to fix nitrogen by $^{15}N_2$ techniques in pure culture (Stewart et al., 1982). The filamentous Microcoleus chthonoplastes, a constituent of King Bay and Nickol River algal mats (Chapter 3), is one of these (Potts, 1979).

Of the environmental factors cited as significant in controlling algal mat nitrogen fixation, water availability appears to be the most important; some algal mats resuming nitrogen fixation within ten minutes of rewetting (Potts, 1979). Other studies have illustrated the importance of moisture to fixation (Jones, 1977a; Stewart et al., 1978; Davey and Marchant, 1983). More recent work has shown that the process of physiological recovery after desiccation in cyanobacteria is rapid, and proceeds in order from respiration (within 30 minutes of rewetting), to photosynthetic oxygen evolution (six to eight hours) and then nitrogen fixation (five to six days,

Scherer et al., 1984). Temperature, a factor related to water availablity, also constrains the fixation activity of cyanobacteria and algal mats (Croome, 1973; Warmling, 1973; Jones, 1977b; 1977e; Gersper et al., 1980; Wickstrom, 1980; Davey, 1983).

Other environmental factors that are significant in controlling fixation in certain localities include light, pH, minor element concentration (Stewart et al., 1978; Gallon, 1980) and the presence of bacteria. Light penetration into an algal mat is markedly reduced close to the mat surface (Reynaud and Roger, 1979), and so there is a fine balance between cyanobacterial survival and decay (Doemel and Brock, 1977; Zinder et al., 1977). At high light intensities, optimum fixation is often observed at some depth in the algal mat (Reynaud and Roger, 1981).

Cyanobacteria are characteristic of alkaline and neutral soils. In cyanobacterial colonies and algal mats from Brazilian, Nigerian and Scottish soils, however, a wide pH tolerance for fixation was found, although all had optima at pH 8 (Stewart et al., 1978).

The presence of non-fixing bacteria may also play an important role in algal mat fixation (Jones, 1977f; Stewart, 1980), chiefly by producing microanaerobic conditions in the mat or colony. In addition, bacteria may aid in the utilization of sulfide as an electron donor for cyanobacterial dark fixation (Gallon, 1980).

Comparatively little work has been done on the effects of salinity on nitrogen fixation in algal mats. The available information suggests that fixation is more sensitive to salinity stresses than is photosynthesis (Tel-Or, 1980). On the other hand some green algae, when placed in high

salinities, are able to adapt by producing organic osmoregulatory solutes (Erdmann, 1983).

The few studies that have examined the significance of algal mat nitrogen fixation, have shown that they make an important contribution to the habitats in which they occur (Burris, 1976; Bohlool and Wiebe, 1978; Goldner, 1980).

The environmental constraints that allow algal mats to competitively exclude other organisms are salinity, desiccation, temperature and low nutrient status. The environments in which algal mats occur are usually oligotrophic (Potts, 1979), so that any input by an algal mat, to this type of environment, is likely to be a significant one. Evidence that cyanobacteria may leach nutrients during growth (Chapters 4 and 5) supports this view, particularly if nitrogen fixation is supplementing a nutrient loss.

6.2 METHODS

The acetylene assay

The acetylene assay gives a measure of the rate of nitrogen fixation of a sample of algal mat. When fixation occurs in the presence of acetylene (C_2H_2) the latter is reduced to ethylene (C_2H_4), which can be quantified by gas chromatography. The affinity of acetylene to nitrogenase is many times greater than that of nitrogen, which ensures that when acetylene is added, nitrogenase reduces it preferentially.

Details of the methods with which acetylene assays were carried out, both in the laboratory and field, are given in Appendix 3.

Determination of acetylene concentration and container size for optimal ethylene production

Two replicates of 2 - 4 g algal mat samples from King Bay, that had been growing for four days in seawater (60 ^{o}/oo, Appendix 1) were placed in six tubes (45 ml) and three flasks (210 ml). Atmospheres in tubes were adjusted to 5% and 10% acetylene in air (vol/vol) and those in flasks adjusted to 10% (vol/vol). One ml (from flasks) and 0.5 ml (from tubes) samples were withdrawn via syringe, every four to eight hours, over a 24 hour incubation period. Vessels were incubated in continuous light in a growth cabinet set at 25 ^{o}C.

Light and dark trials

Throughout 1983, at the Botany Department, University of Western Australia, assays were done on King Bay and Nickol River algal mats that had been growing in standard seawater (36.4 ^{o}/oo). In all cases these were carried out in tubes (45 ml) with 10% acetylene in air (vol/vol) and incubations were in a natural light glasshouse.

For these trials the 'dark' tubes were wrapped in silver foil, leaving the seal free for injection purposes. Both light and dark samples were incubated in the glasshouse or a 25 ^{o}C laboratory.

Salinity and light trials

From each of the salinity and light levels examined (Chapter 4), four pairs of algal mat cores (19 mm diameter) were placed in incubation vessels, sealed and acetylene added to three of these to make a 10% volume of acetylene in air. One vessel from each level was used as a control. These were incubated over a period of 24 hours, in a natural light glasshouse for the salinity trials, and at each light level for the light trial.

Carbon dioxide production

The production of CO_2 was measured from the control (i.e. minus acetylene) vessels incubated for the salinity trial described above. Three replicate gas samples were withdrawn by syringe from each vessel and analysed for CO_2 using a Series 225 Gas Analyser (Analytical Development Co.) set at 20 mV FSD and calibrated with a 1% (10,000 ppm) CO_2 standard.

Rewetting trials

Two to four gram samples from King Bay mat that had been air dried for two months were placed in tubes containing 3 ml of seawater ($36.4^{o}/oo$). These were sealed and acetylene added to make a 10% atmosphere every three hours over a 24 hour period and six hours thereafter for a further day. Three replicate mat samples were used for each assay. The ethylene content of each assay was determined by 1 ml injections (three replicates) from each container 24 hours after each assay was commenced. A similar assay, not including seawater, was set up for control purposes.

Algal mat that had been stored in a cool room for three months was placed in standard seawater ($36.4^{o}/oo$) and ethylene production measured after one day. A control mat that had not been inundated was also measured.

Field sampling

Measurements in the field were performed by placing 2 - 4 g samples of algal mat (removed with a scalpel), from various points at King Bay and Dampier Salt, in assay vessels. Three replicates and two controls were used at each point examined. These were incubated <u>in situ</u> by replacing them in the sediment, from which the mat had been taken, and securing them by lead weights to prevent flotation on high tides. These were retrieved after 24

hours, and measured in the field laboratory on the L and D Portable GLC. Points examined within sites included 'wet', 'dry' and friable mats along the transect at Dampier Salt, and various points within the King Bay system before and after tidal inundation.

6.3 RESULTS

Acetylene concentration and container size

Linear production of ethylene occurred between 0 and 10 hours in tubes (45 ml) containing 10% acetylene (Figure 6.1) and 2 - 4 g algal mat. The rate between these times was 67.5 umoles C_2H_4 produced m^{-2} hr^{-1}. Ethylene production was less in 5% acetylene and the flasks, indicating that the calculated reduction rates for 24 hour incubations were approximately one-half of the initial rate which would have been obtained in tubes.

Salinity and light effects on fixation

Algal cores from King Bay and Nickol River showed high rates of acetylene reduction at a salinity range of 20 - 60 $^{o}/_{oo}$, but rates were low at 0 $^{o}/_{oo}$ and above 100 $^{o}/_{oo}$. Little or no activity could be detected at either site above 120 $^{o}/_{oo}$ (Figure 6.2).

There was no detectable activity after 24 hours or 36 hours in algal cores subjected to different light levels.

Carbon dioxide production

Carbon dioxide production in King Bay algal mats decreased with increasing salinity (Figure 6.3) and those from Nickol River showed an optimum at 20 $^{o}/_{oo}$ salinity. Mats from Nickol River generally had higher rates of CO_2 production.

Rewetting trials

There was no measurable rate of acetylene reduction in algal mats that had been dry for two months. After two and a half days of immersion, low rates were recorded (1 umole C_2H_4 produced m^{-2} hr^{-1}) but fixation was not detectable thereafter. Algal mats that had been under cold storage (6 °C) did not fix until they had been immersed. After one day, rates of 2.72 (± 0.32) umoles C_2H_4 produced m^{-2} hr^{-1} were recorded.

In situ acetylene reduction

Considerable difficulties were experienced in measuring acetylene reduction in the field laboratory, most stemmed from electronic perturbations of the Portable GLC. Results obtained from King Bay showed few differences between the points measured (Figure 6.4); rates ranging from 6 to 9 umoles C_2H_4 produced m^{-2} hr^{-1}.

General

Mats from King Bay, in the dark, produced ethylene at a rate of 0.311 (± 0.16) umoles C_2H_4 produced m^{-2} hr^{-1} which was approximately 60% of the rate shown by samples incubated in the light (0.526 ± 0.09).

Rates measured in situ at King Bay and Nickol River throughout 1983 varied, but were generally in the range of 8 - 16 umoles C_2H_4 produced m^{-2} hr^{-1} in mats.

6.4 DISCUSSION

The laboratory conditions in which optimal acetylene reduction rates in algal mats occurred, ie. salinities between 20 and 60 °/oo (Figure 6.2), correlate well with conditions that existed at each site. Tidal water generally inundated the mat at 35 - 40 °/oo and left at 40 - 60 °/oo (Chapter

5). Significant fixation rates that occurred outside this range indicate that there may have been a wide salinity tolerance in the field. Thus, fixation may occur as the algal mat dries, between tidal cycles, and the salinity increases as salt crystallizes on the mat surface. Tel-Or (1980) recorded lower tolerance ranges for fixation than for photosynthetic activity in Nostoc and Calothrix species. The increase of algal mat chlorophyll a, over the range of salinities tested (Chapter 4), supports this view.

Nitrogen fixation is usually the last physiological process to resume in cyanobacteria when rewetted after periods of desiccation (Scherer et al., 1984). The ability of Dampier algal mats to reduce acetylene within two and one-half days of immersion, indicates an adaptation to the extreme environment. In the field mats would be dry for a maximum period of seven days. The cyanobacteria studied by Scherer et al. (1984) resumed fixation six days after rewetting. Algal mats in other tropical systems are able to absorb enough moisture from dew to fix nitrogen until noon, when they dry out (Stewart et al., 1978). Perhaps unbroken mats of the Dampier coastline (with a water content of 40% - Chapter 4) may also be able to fix nitrogen when not directly immersed.

Comparatively high rates of acetylene reduction in the dark has suggested to other workers that dark fixation may be supported by a source of dark-generated reductant (Stewart, 1973). Potts (1979) however, explained dark reduction as a result of diminishing competition between acetylene reduction and photorespiration. In this study, dark reduction took place at a rate 60% of that observed in light. Whether CO_2 production recorded in the light (Figure 6.3) was caused by cyanobacterial photorespiration, rather than

bacterial respiration, is not known. The influence of bacteria in algal mats has been little studied (Jones, 1977f; Stewart, 1980), although hydrogen production observed in decomposing mats has been contributed entirely to them, rather than cyanobacteria (Oremland, 1983). The ability of bacteria, like Azotobacter (Dicker and Smith, 1981), to fix nitrogen as well as respire at salinities of 10-20 $^{o}/_{oo}$, also suggests that bacteria may influence the acetylene reduction activity of those mats in which they occur.

Little information was derived from the light trial. Stal et al (1984), using algal mats with species compositions similar to those found in this study, has reported that low light intensities appear to stimulate nitrogenase activity. These workers found optimal fixation at sunrise and sunset. Clearly in situ studies are necessary to determine the effect of light intensity on Dampier algal mat fixation in the short and long-term.

To convert acetylene reduction data into actual fixed nitrogen figures, a conversion factor is needed. Theoretically, two electrons are used to convert acetylene to ethylene, while six electrons are needed to convert one molecule of nitrogen to ammonia. Therefore a conversion factor of three is required. This factor has been used in this study to give a generous estimate of nitrogen fixed. In other cyanobacterial and algal mat studies however, higher conversion factors have been used; they have ranged from 3 to 5.4 (Flett et al., 1976; Stal et al., 1984). This is because some electrons used by nitrogenase reduce protons (H^+ to H_2) rather than nitrogen. The number of electrons used in this way may vary from 0 to 60% of the total passing through the nitrogenase system (Stewart et al., 1982). Because there is usually little H_2 production, by nitrogenase, under an acetylene atmosphere (Stewart, 1980), the theoretical conversion factor of three may be overestimating the acetylene-reduced to nitrogen-fixed ratio.

It is also necessary to take into account the underestimation of acetylene reduction in the 24 hour incubations used in this study. Data derived from 24 hour incubations are likely to be one-half of the actual figure. If the above factors are taken into account the *in situ* range for fixation becomes 12 - 32 umoles C_2H_4 produced m^{-2} hr^{-1} which is 56.0 - 149.3 mg N m^{-2} hr^{-1} (0.59 - 1.58 kg N ha^{-1} yr^{-1}) and under optimum conditions (in the laboratory) is 2.2 - 3.0 mmoles C_2H_4 produced m^{-2} hr^{-1} (10.27-14.00 mg N m^{-2} hr^{-1}) which becomes 108.8 - 148.4 kg N ha^{-1} yr^{-1}.

In the field algal mats are inundated for approximately four to six hours a day for 67% of the year (245 days in 1983, see Chapter 5) and are exposed for two to seven days between tidal cycles. Clearly, *in situ* assays, which are supported by rates measured in the laboratory throughout the year, are probably a better representation of fixation than rates recorded under optimum conditions. Thus, based on *in situ* rates, the 0.51 ha of algal mat of King Bay would fix approximately 0.3 - 0.8 kg of nitrogen per year. These rates agree well with other algal mats in similar environments (Table 6.1), but in a system with a comparable, non-heterocystous, species composition (Stal *et al.*, 1984), rates were ten times that of Dampier mats. The large difference between *in situ* fixation rates and those under optimum experimental conditions, illustrates the considerable fixation potential of these mats.

Further study involving the separation and axenic culture of cyanobacteria from these algal mats is required before the influence of bacteria and physical factors can be assessed. Similarly more complete *in situ* studies on temporal and spatial variation, particularly in regard to desiccation and tidal inundation, are needed to fully document the nitrogen fixing potential of the Dampier algal mats.

Table 6.1 Algal mat acetylene reduction and nitrogen fixation rates recorded for various studies. More extensive list may be found in Warmling (1973), Potts (1979) and Goldner (1980).

Dominant Cyanobacterial Species Or Associations *1	Time Course For Incubation (hours) *2	Reported Rate	Study
Oscillatoria-Euglena- Photosynthetic bacteria	24	83 um C_2H_4 prod.$m^{-2}hr^{-1}$	Bohlool & Wiebe, 1978
Microcoleus (in situ)	24	12-32 "	This study.
Microcoleus and Phormidium (laboratory)	24	16-120 "	"
Microcoleus (20^{o}/oo salinity)	24	2200 "	"
Phormidium (20^{o}/oo salinity)	24	3000 "	"
Microcoleus-Oscillatoria (II)	4	205±36 "	Stal et al., 1984
Microcoleus-Oscillatoria (III)	4	641±107 "	"
Oscillatoria-Spirulina-Gleocapsa (I)	4	42±3.8 "	"
Nostoc spp. (in dark)	1	6000 "	Jones, 1977b
Anabaena spp. (cylinders)	0.5	5800 "	Traore et al. 1981
Anabaena spp. (bottles)	0.5	2100 "	"
Blue-green algal communities	-	1.1-4.0 X 10^5nmol N_2 $m^{-2}hr^{-1}$	Goldner, 1980
"	-	2.25-12 X 10^4nmol N_2 $m^{-2}hr^{-1}$	"
Gleocapsa-Oscillatoria (0^{o} C)	1	18 ug N_2 m^{-2}	Warmling, 1973
Lyngbya (0^{o} C)	1	140 ug N_2 m^{-2}	"
Calothrix-Gleocapsa-Phormidium	1	11 mg N_2 m^{-2}	"
Oscillatoria-Lyngbya-Anabaena	1	50 ug N_2 $m^{-2}hr^{-1}$	Smith & McLachlan, 1979

*1
Conditions described in brackets.
*2
- denotes not stated.

6.5 SUMMARY

- Algal mats from King Bay and Nickol River have the potential to fix nitrogen at high rates. Under optimum laboratory conditions (high water availability and low salinity) mats produced ethylene at 2200 - 3000 umoles C_2H_4 m^{-2} hr^{-1} (10.27 - 14.00 mg N m^{-2} hr^{-1}).
- In situ studies show that this potential is probably not realised in the field where production rates of 12 - 32 umoles C_2H_4 m^{-2} hr^{-1} (56.0 - 149.3 ug N m^{-2} hr^{-1}) were recorded.
- Mats were able to reduce acetylene within two and one-half days of immersion after a period of dehydration.
- The presence of moisture in algal mats suggests that fixation could occur when mats are not directly immersed by the tide.
- Mats were able to reduce acetylene at salinities ranging from 0 to 120 $^{o}/_{oo}$ with optima between 20 and 60 $^{o}/_{oo}$. This supports the view that mats may fix nitrogen when uncovered between tidal cycles, as well as during tidal inundation.
- King Bay was estimated to receive approximately 0.3 - 0.8 kg of nitrogen per year from algal mat fixation (at a rate of 0.59 - 1.58 kg N ha^{-1} yr^{-1}). The actual figure may be higher as mats may fix when not directly immersed.

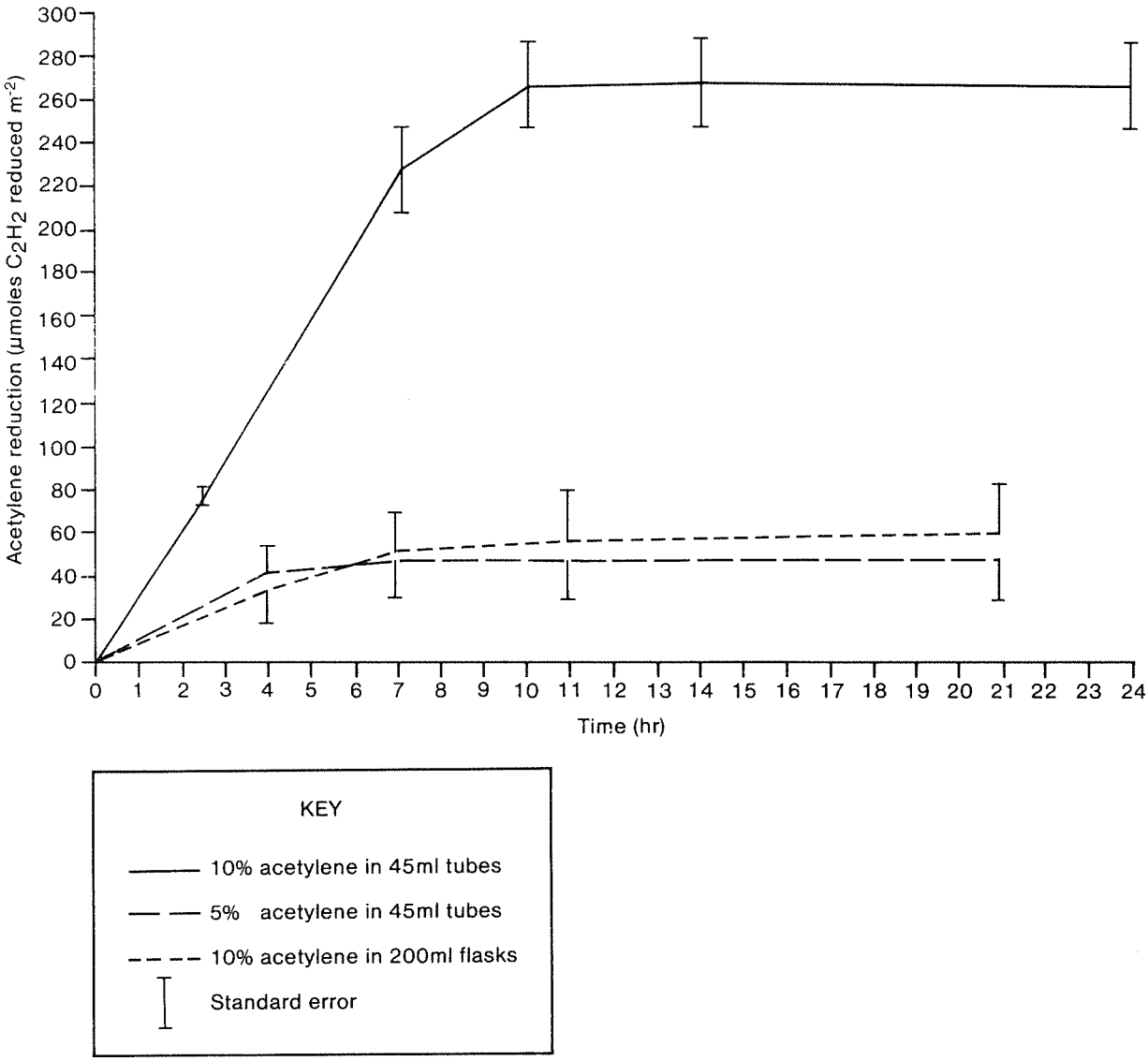


Figure 6.1 The effect of container size and acetylene concentration on ethylene production over a 24 hour period.

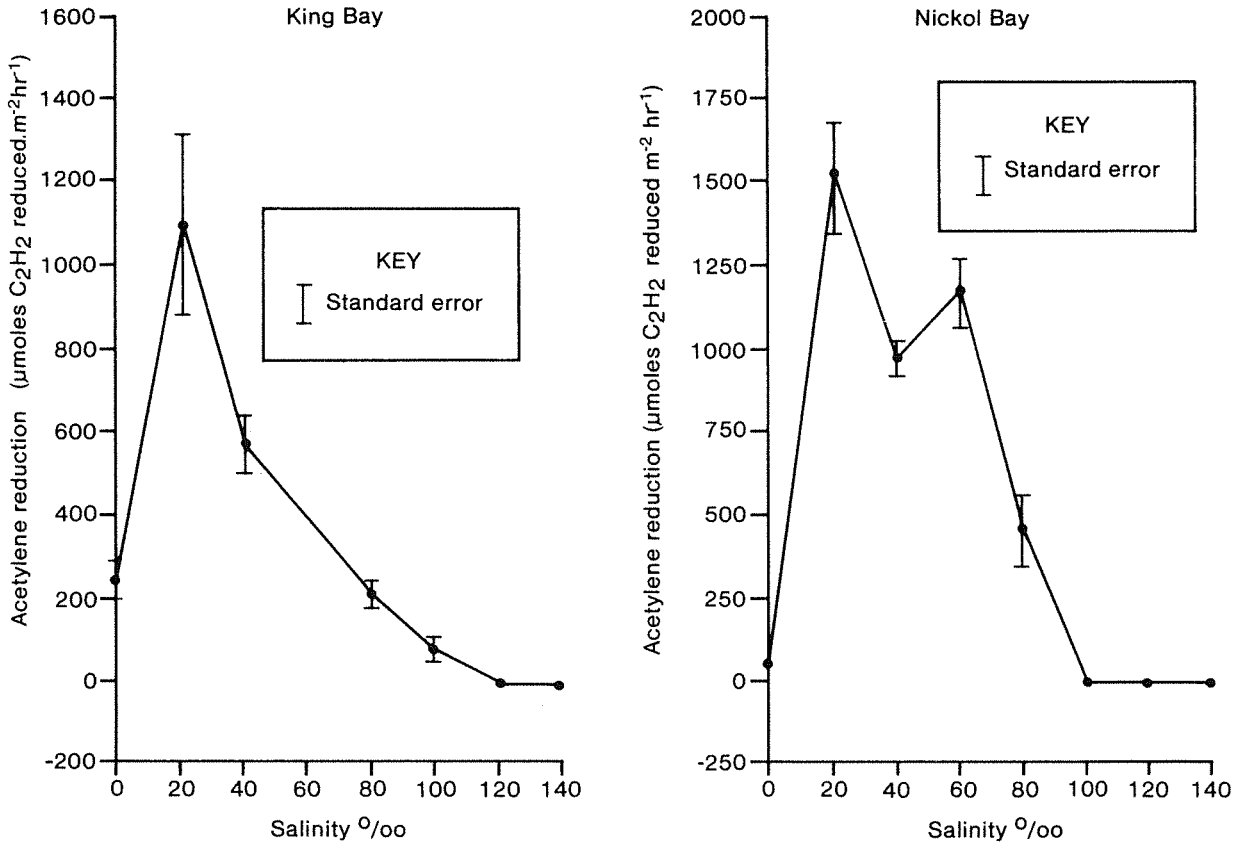


Figure 6.2 The effect of salinity on acetylene reduction in glasshouse trials of King Bay and Nickol River algal mats.

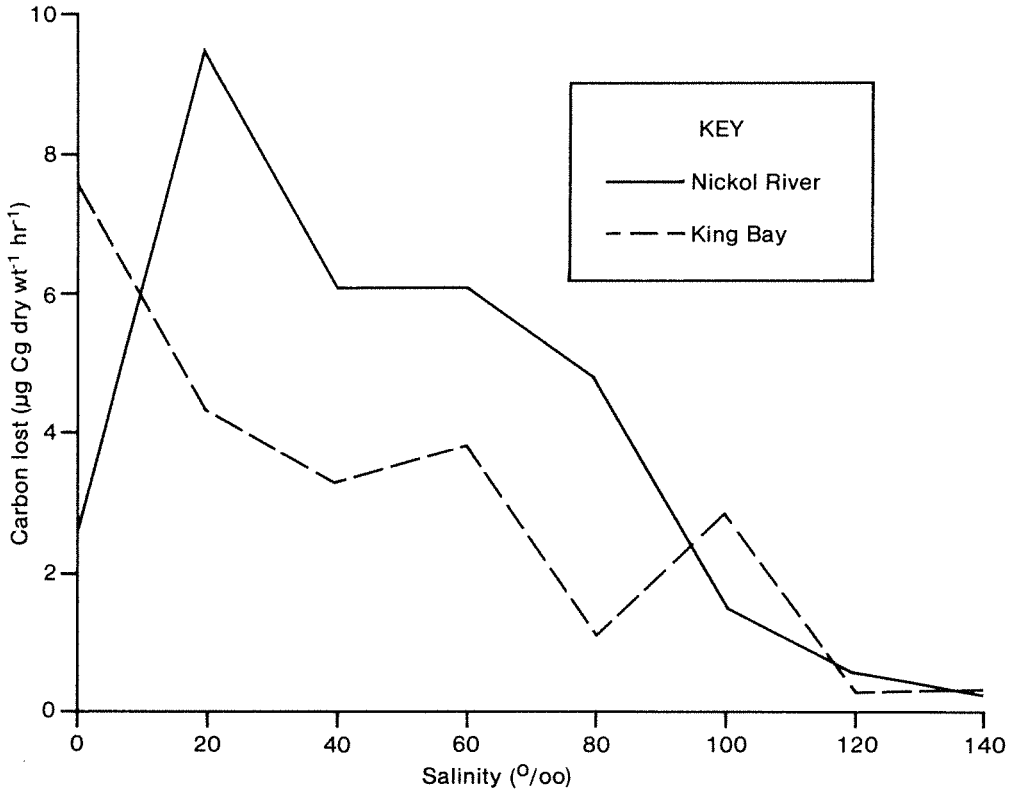


Figure 6.3 Carbon lost as CO_2 by algal mats grown at various salinities after 24 hour incubations.

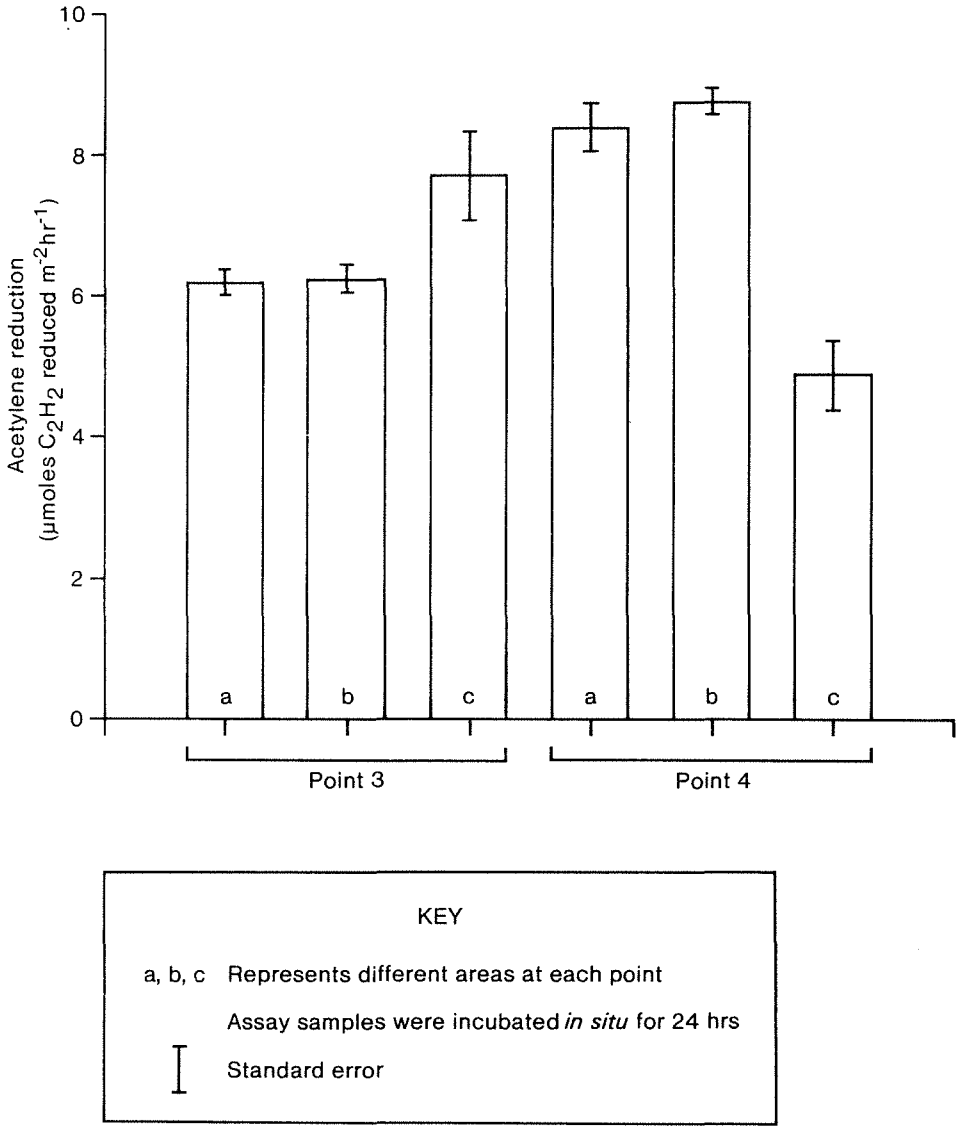


Figure 6.4 *In situ* nitrogen fixation measured as acetylene reduction at two points at the King Bay site.

7. GENERAL DISCUSSION

7.1 ALGAL MAT GROWTH

On the Dampier coastline there appeared to be three major, interacting factors which influenced the distribution and seasonal productivity of algal mats: the tidal height, the degree of tidal current and sediment influx, and the conditions of drainage. These in turn would be expected to influence other factors, for example salinity. Thus algal growth and mat morphology was affected by the gradient in water supply, which resulted from a combination of the total time of submersion and the subsequent extent of evaporation.

The upper limit of algal mat distribution could therefore be attributed to the shortage in water supply which varied according to season, climate and wind exposure, while the lower limit was probably determined by sediment instability, grazing and burrowing crabs and erosion.

Different hydrologic conditions existed at each site (Chapter 4) and these appeared to determine the rate of mat growth. At King Bay, the higher proportion of sand in the algal mat showed that there was a large degree of sediment influx which, combined with grazing crustaceans, hampered regrowth. Similar regrowth and mat structure occurred at Dampier Salt as at Nickol River, both of which had a higher carbon content (Chapter 4) than King Bay. The reason for this being the lower sediment influx, which, combined with increased water availability, produced mats with little combined sediment.

The occurrence of 'wet' and 'dry' mats at Dampier Salt and Nickol River (Chapter 3) indicated that water may pond in minor depressions on the mat surface, and then slowly evaporate causing both increased salinities and raised temperatures which markedly affected the structure of the mat. At

Dampier Salt this occurred to an extreme degree and reduced the mat species diversity such that the centres of these depressions were covered by bare sand, and only Phormidium was present at the edges.

The lower water content of 'wet' mats (29%, Table 4.3) was probably caused by their open structure which, combined with their lack of sediment, allowed them to dry out rapidly and produce friable portions of mat that could be transported by wind. Friable mats at King Bay were derived from tidal erosion and disturbance from the public that had access to the area; factors which increased the rate of desiccation of the mats (Chapter 2).

Studies on spatial variation in growth at each site revealed the tendency for higher levels of chlorophyll and organic carbon to occur at areas with greater water availability. The measurement of these factors, and dry weight, are useful for determining the long-term status of the mat with regard to environmental variables. But only measurements such as regrowth, acetylene reduction or chlorophyll production, per unit time, can give a true indication of the turnover of algal mat biomass.

Seasonal variation in mat structure appeared to be caused by the climate. Lower temperatures and evaporation lead to increased water availability, particularly at Dampier Salt and Nickol River, and hence greater growth in winter. King Bay mats changed little over the year, suggesting that water availability and sediment influx remained relatively constant.

Chlorophyll production and acetylene reduction occurred over a wide range of salinities under conditions of high water availability and lower temperatures in the glasshouse (Chapters 4 and 6), which suggests that a wide tolerance might also exist in the field.

Increased metabolism during tidal immersion (Chapters 3 and 6) showed that the mat cyanobacteria recovered rapidly after short periods of desiccation (Chapter 4).

7.2 ECOLOGICAL SIGNIFICANCE

The algal mats at Dampier bound substrate and stabilized the surface, reducing erosion of the tidal flats. Despite the arid environment, they could conserve water (29 - 47%) and thus acted as an 'ecological membrane' preventing the desiccation of microorganisms living within and beneath the mat. Metazoans grazed on the mat, which clearly represented part of the food chain. The mats were rich in organic matter and served as a store of carbon (500 - 800 g m^{-2}), nitrogen (14 - 21 g m^{-2}) and phosphorus (0.7 - 1.5 g m^{-2}). These levels are comparable with algal mats in other systems (Chapter 4; Whittaker and Likens, 1975). Friable portions of mat contained 25% of the organic carbon present in normal mats, and one third of their nitrogen content.

These mats fixed nitrogen at low rates in the field (12 - 32 umoles C_2H_4 produced m^{-2} hr^{-1}) but showed a high potential under optimum laboratory conditions. Chlorophyll production could be as high as 7.4 mg chlorophyll *a* m^{-2} d^{-1} under similar conditions.

Algal mats are usually reported as being a significant source of nitrogen (derived from fixation) in ecosystems in which they occur (Chapter 6), particularly salt marshes (Valiela and Teal, 1979; Smith *et al.*, 1982; Whitton and Potts, 1982) and mangroves (Potts, 1979). Most high rates of fixation are recorded in mats that contain heterocystous cyanobacteria. So far, two suggestions have been put forward to account for the differential

distribution of non-heterocystous and heterocystous genera. Potts (1980) has suggested that greater nutrient availability aids the development of non-heterocystous forms, and Stal et al. (1984) has suggested that heterocystous algae are unable to tolerate changing environmental conditions or high sulfide concentrations. The occurrence of only non-heterocystous cyanobacteria in Dampier algal mats may, therefore, result from the extreme environment which has high temperatures, high salinity and reduced water availability. Further study is required before this can be confirmed.

7.3 NUTRIENT EXPORT

Leaching studies on friable mat from King Bay and Dampier Salt showed losses of up to 250 mg N m^{-2} over a short time period when immersed (Chapter 5), and therefore a possible avenue of nutrient loss (via leaching) when still connected to the main algal mat. In addition loss of both carbon and nitrogen may occur when sections of mat are transported in solid form from the system.

Considerable leaching of nutrients occurred into freshwater. Large quantities of nitrate were lost from algal mat segments from King Bay and Dampier Salt in May, 1983. But in July, particulate organic nitrogen was the major form leached. Greater leaching occurred in areas where water was not readily available, indicating that desiccated mats, particularly, were less able to prevent loss. Thus rainfall is likely to leach nutrients as it percolates through mat and sediment, and into tidal creeks. Most rainfall in the Dampier Archipelago occurs in summer when nitrate is the nutrient most likely to be lost. As most of the nutrient loss into freshwater occurred in less than eight minutes (Chapter 5), losses occurring through rainfall are likely to be high.

Considerable quantities of particulate organic nitrogen and phosphorus, probably derived from dead organic material or living cells, were transported from the mat in the field enclosure. Information from leaching experiments showed that algal mats were capable of both leaching to seawater and freshwater, and absorbing from freshwater, large quantities of nutrients (e.g. nitrate), within 60 minutes (Chapter 5). This raises the possibility that algal mats may absorb nutrients when they occur in high concentrations in seawater.

The major findings of this work were that algal mats in these systems contained relatively large amounts of carbon, nitrogen and phosphorus. Of these, nitrogen and phosphorus could be leached by rainfall and tidal water. Leaching losses, may have been overestimated in this study (Chapter 5), as nutrients may have been simultaneously leached and absorbed by different areas of mat.

High metabolic rates were recorded under optimum laboratory conditions. Rapid regeneration and growth also took place in the field (Chapters 3 and 4). These observations suggest that there was rapid turnover of algal biomass on the salt flats. The large quantities of nutrients leached indicates that algal mats may be inefficient at preventing nutrient loss during some stages of their growth cycle, and when desiccated.

Bearing in mind the spatial and temporal limits that control leaching and fixation, it is possible to calculate theoretical losses that may occur from algal mats in a system. The loss of nitrogen in King Bay is used below as an example.

The total nitrogen content of King Bay mats was estimated at 70 kg (Chapter 4) and losses were estimated at 34 kg of particulate organic nitrogen per year (Chapter 5). The rate of nitrogen input from fixation into King Bay was found to be 0.301 - 0.806 kg per year (0.59 - 1.58 kg N ha^{-1} yr^{-1}) (Chapter 6). This is clearly insufficient to replace probable losses via leaching. However, if experimental rates obtained under optimum conditions, are used, 55.5 - 75.7 kg of nitrogen could be added each year (108.8 - 148.4 kg N ha^{-1} yr^{-1}). Without more field data it is not possible to determine the changes in fixation rates which may take place both seasonally and on a short-term basis. Mats may be fixing nitrogen not only when immersed, but between tidal cycles. Stal et al. (1984) concluded that mats which they studied fixed nitrogen for six months out of each year, and for 24 hours a day during this time, producing 4.4 - 24.4 kg N ha^{-1} yr^{-1}.

Mangrove sediments are known to be active in the uptake of carbon, nitrogen and phosphorus (Hesse, 1961; Lugo and Snedaker, 1974; Boto and Bunt, 1981; Boto, 1982), but the hydrology of each individual site in the Dampier Archipelago would determine whether or not nutrients would be available to the mangrove sediments. King Bay was the only study site at which algal mat occurred adjacent to mangroves. In other areas mangroves were distant, and flushing from the mat would proceed via tidal creeks rather than over the mangrove sediments.

In conclusion, there was evidence that the algal mats on the salt flats associated with mangroves in the Dampier Archipelago, could have lost significant amounts of nutrients, mainly nitrogen in particulate form, to tidal water. Nitrogen fixation in these systems however, may not have been sufficient to replace this loss, indicating that outside sources of nitrogen, as well as of phosphorus existed to maintain mat biomass.

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APPENDIX 1

ARTIFICIAL SEAWATER MEDIUM USED FOR CULTURING ALGAL MATS

Appendix Table 1 Chemicals and their concentrations for the artificial seawater medium used for culturing algal mats in this study. Modified from Gordon et al. (1980).

Salt Block *1	Chemical	Concentration ($g\ L^{-1}$)
	NaCl	166.17
	KCL	4.15
	$MgSO_4$	41.54
	$MgCl_2 6H_2O$	23.74
	Ca (as Cl^-)	2.37
Nutrient block *2	NH_4NO_3	1.430×10^{-2}
	K_2HPO_4	1.405×10^{-3}
	$NaHCO_3$	0.2
	$Na_2SiO_3 9H_2O$	1.5×10^{-2}
Buffer *1	Tris	5.934

*1 Concentration necessary for 200 $^{o}/_{oo}$ salinity, this was subsequently diluted for the range of salinities tested.

*2 Nutrient block was added to each medium at concentrations necessary for 33.7 $^{o}/_{oo}$.

APPENDIX 2

CALCULATION OF VOLUME FLUX AND ITS USE FOR CALCULATING NUTRIENT FLUXES IN THE KING BAY ENCLOSURE

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Volume Estimation. The height to volume ratios were determined by simple geometry (see Appendix Figure 1):

(i) The volume change before the tide had reached the back of the enclosure ('A' in Appendix Figure 1). For example, at 0 cm there is 0 volume in the enclosure, at 1 cm there is 1 cm (h) x 1 m (width) x 1.7 m (length) x 1/2

$$= 1/2 \times 0.01 \times 1.7$$
$$= 0.0085 \text{ m}^3 \quad (1 \text{ m}^3 = 1000 \text{ litres})$$
$$= 8.5 \text{ L}$$

By using height data for the water level when the back of the enclosure had been reached, it was calculated in a similar way, that 1063 L of water had entered the enclosure.

(ii) To determine the volume change after this period ('B' in Appendix Figure 1, a simple L x B x H calculation is performed and added to A (1063 L). The volume/height ratio in this enclosure was linear (Appendix Figure 2). Thus, volume curves were generated for each tidal cycle. These curves were subsequently smoothed to accommodate the measurement of instantaneous flow rates.

Instantaneous flow rates. These were calculated by taking the volume change over a measured time interval. Thus, a decrease in volume (tidal ebb) produces a negative instantaneous flow rate. Flow rates for each tidal cycle were graphed.

From these curves the flow rates were read off (in L min-1) for the times that water samples were taken from the entrance of the enclosure.

The volume flux within the enclosure was checked to determine whether similar volumes of water entered and left on each tidal cycle. This was done so that confidence estimates of mass nutrient flow could be calculated. The difference between the calculated volume of water entering and leaving the enclosure was generally less than 6%, and it was concluded that instantaneous flow rates would provide a valid way to calculate mass nutrient, salinity and oxygen flux.

Calculation of mass nutrient flux. An example is given for NH_4-N on the 9.7.83 to illustrate the method of calculation (Appendix Table 2). Once the instantaneous mass flux had been calculated (ug min^{-1}), then total mass flux (ug) was estimated by assuming that the instantaneous flux represents the flux over the time period between the collection of this sample and the collection of the previous one. The mass flow over each time period is shown in Appendix Table 2.

Once this had been accomplished for each nutrient on each cycle, mass fluxes were calculated for the enclosure by adding all positive values (representing input; water flowing in) and all negative values for export (water flowing out). Using NH_4-N (mg):

Import = 0 + 1.77 + 0.11 = 1.89 (0.35)

Export = (-0.38) + (-0.88) + (-0.40) + 0 = -1.66 (0.58)

Thus on the 9.7.83, 1.89 mg came into the enclosure and 1.66 mg went out, a net flux of +0.22 mg.

Appendix Table 2 An example of the calculation of mass nutrient flux in the enclosure at King Bay using ammonia on the 9.7.83.

Time* (min)	Time interval	Concentration $\bar{x}$ (SE) (ug L^{-1})	Flow rate (L min^{-1})	Instantaneous mass flux (ug NH_4-N min^{-1})	Mass over time period (ug $\bar{x}$ (SE))
0	0	2.80 (0.43)	0+	0	0
23	23	1.75 (0.32)	44	77	1771(322)
46	23	1.25 (0.32)	4	5	115(30)
66	20	2.37 (0.55)	-8	-19	-380(88)
76	10	1.62 (0.47)	-54	-87.7	-877(250)
86	10	1.12 (0.88)	-36	-40.5	-405(240)
101	15	-	0	0	0

* Water samples taken

+ Little water in enclosure

APPENDIX 3

THE ACETYLENE REDUCTION ASSAY

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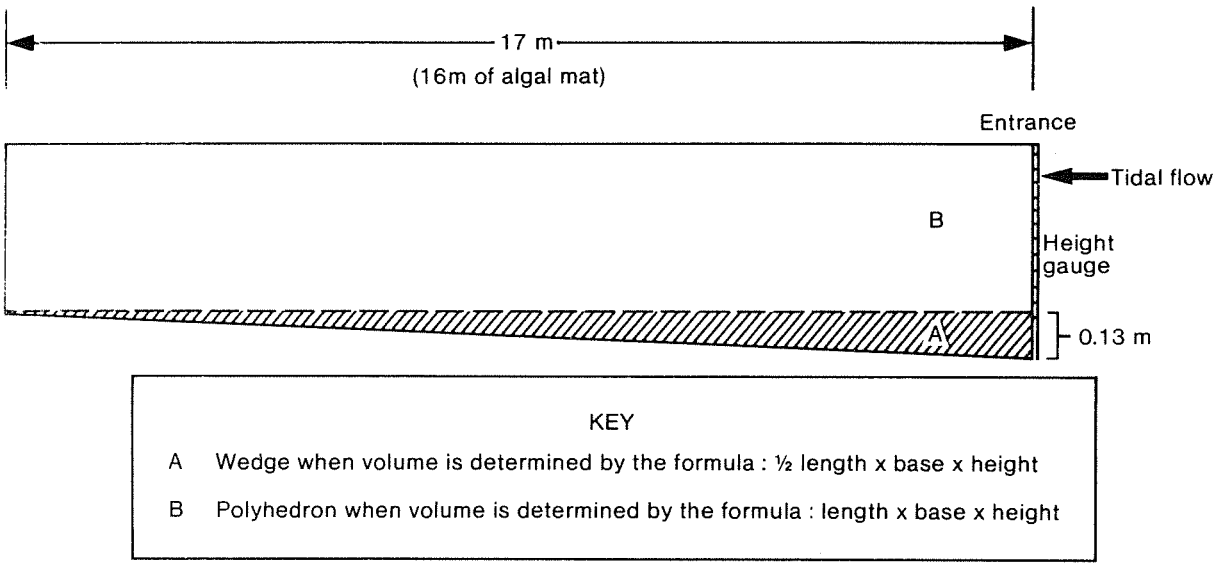
THE ACETYLENE REDUCTION ASSAY

Laboratory. All assays unless otherwise stated, were conducted using 45 ml glass tubes sealed with Suba-Seal #45 rubber stoppers and containing 10% acetylene in air (vol/vol). These were incubated for 24 hour periods using approximately 2 - 4 g (dry weight) of algal mat. Salinity and light trials used approximately 1.5 g (dry weight) algal cores. All results were converted by the appropriate factor, to ethylene (C_2H_4) produced m^{-2} hr^{-1} taking into account weight/area relationships for algal mats at the different sampling points.

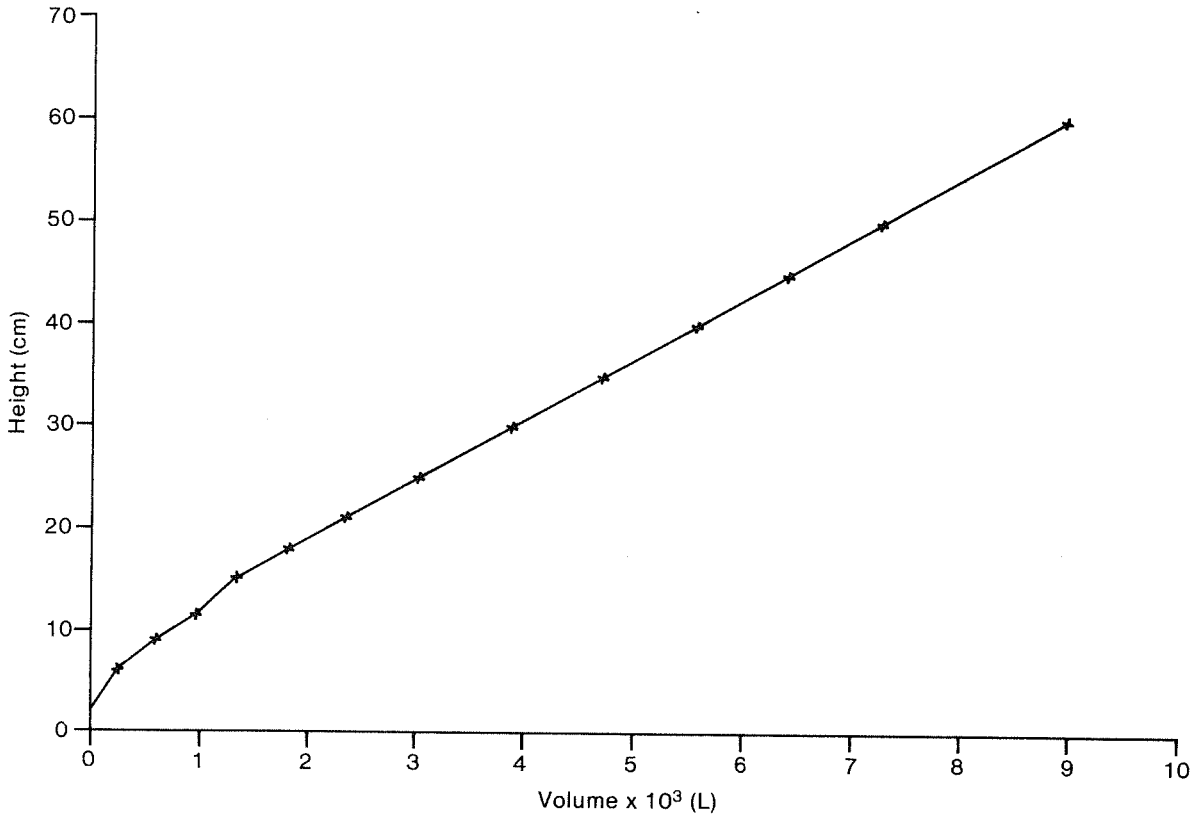
The ethylene concentrations of 0.5 and 1.0 ml gas samples (three replicates) removed from incubated vessels by syringe were analysed on a Shimadzu GC-6AM Series Gas Chromatograph using a flame ionization detector (FID-6M) incorporating a 3.5 mm O.D. x 2 mm I.D. x 1 m column packed with 100 - 120 mesh Porapak T. The column was run at 100 ^{o}C, with argon as the carrier gas flowing at 35 ml min^{-1}, using a hydrogen/air flame. Peak height calibration was performed using 0.5 and 1.0 ml injections of a 133 nm ml^{-1} ethylene standard. In all assays control vessels containing algal material were incubated without acetylene and these did not produce significant amounts of ethylene. No ethylene contaminants were observed in the blanks, containing acetylene only, which accompanied all assays.

Field. Field assays were performed on an L and D Portable GLC using a TGS gas-sensitive, semi-conductor incorporating a 1.5 mm I.D. x 1 m teflon stainless steel column packed with Porapak T. The column was run at ambient temperatures with a column head pressure of 60 kPa. Peak height calibration

was performed using 1 ml injections of a 70 nm ml^{-1} ethylene standard, and controls were identical to those described above. The Portable GLC was housed in the Dampier Field Laboratory, Department of Conservation and Environment, throughout the field assays.



Appendix Figure 1 Surface elevation of the enclosure (not to scale).



Appendix Figure 2 Volume changes with height of water in the enclosure, July, 1983.