Salt ponds of the British Virgin Islands:

Investigations in an unexplored ecosystem

by

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Abstract

Salt ponds occur within the coastal mangrove forests of Caribbean islands, where they are threatened by coastal development. Despite extremes of salinity, temperature and dissolved oxygen, these ponds support highly productive aquatic communities upon which most waterbirds depend. Salt ponds also provide valuable services, such as trapping sediments and nutrients that can damage near-shore marine ecosystems. Nevertheless, salt ponds have received little scientific attention, resulting in a misunderstanding of their ecosystem services and little guidance for their appropriate management.

This thesis presents an ecosystem characterization, based on extensive sampling of hydrological, chemical and biological parameters in salt ponds of the British Virgin Islands. Sampling results showed levels of temporal and spatial variation previously undescribed in mangrove habitats. Patterns of variation among ponds indicated at least 3 distinct types of ponds and reflected a geological transition from open lagoons through successive pond stages with increasing isolation from seawater.

Pond salinities fluctuated in response to seasonal evaporation and precipitation patterns. Mean salinities in most ponds ranged from 52 ± 33 to 160 ± 69 ppt. Populations of widely-distributed aquatic taxa responded to temporal salinity variations. Most taxa did not occur at salinities above 120 ppt, but a few tolerated salinities greater than 150 ppt. High-salinity species were generally absent, due to predatory and competitive interactions, at salinities below 70 ppt. Transitions between communities of high-salinity and low-salinity taxa occurred at salinities between 75 and 110 ppt.

Salinity fluctuations and community responses were not synchronized among ponds, leading to a shifting mosaic of aquatic populations. Waterbirds depended on these fluctuating prey populations and regularly moved between ponds. These findings showed that salt ponds exist as a network of habitats within a wider ecosystem. As a result, effective conservation efforts must protect a full range of salt ponds rather than individual ponds.

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Chapter 1: Introduction

This thesis reports on a long-term study of salt ponds in the British Virgin Islands (BVI), a small archipelago at the eastern end of the Greater Antillean island chain in the Caribbean (Figure 1.1). The study's goals were to identify the members of salt pond communities and to describe patterns of biological, chemical and hydrological variation within and among BVI salt ponds.

Figure 1.1 Location of the British Virgin Islands in the Caribbean Sea

1.1 A definition of salt ponds

Coastal seawater ponds accumulate sea-salts by evaporation, particularly in regions where precipitation is low. The best known of these hypersaline (more saline than seawater) habitats are salterns that have been artificially created for salt production in many parts of the world, but their naturally occurring counterparts, called "salt ponds", are common features of mangrove wetlands in the Caribbean (Scott & Carbonell 1986). As an ecosystem, a salt pond includes not only the hypersaline aquatic habitat but also the pond shoreline and its fringing mangrove forest.

Hypersaline water bodies also form inland and are common in dry continental areas (Williams 1993), but unlike salt ponds, they contain salts and minerals derived from terrestrial deposits or from ancient ocean salt deposits. A salt pond ecosystem is defined in this thesis as a hypersaline water body fringed by mangrove trees and having minimal direct exchange with seawater yet retaining salts of marine origin. The global distribution of salt ponds is generally restricted to warm, dry coastal areas, where precipitation is insufficient to flush out accumulated salts.

1.2 The value of salt pond ecosystems

Historically, BVI salt ponds and their mangrove forests were of direct economic value to BVIslanders who used mangrove wood for charcoal and boat building, hunted ducks, trapped great land crabs (*Cardisoma guanhumi*) and extracted salt from ponds. Today, these activities are more common on other Caribbean islands (Scott & Carbonell 1986). More significant, however, are the indirect benefits of salt ponds to Caribbean communities. Salt pond ecosystems and their associated mangrove forests provide storm protection and flood mitigation, shoreline stabilization, erosion control, and retention of nutrients and sediments (Barbier *et al.* 1997; Hamilton 1984). These indirect services are largely unrecognised, a predicament shared by wetlands worldwide (Barbier *et al.* 1997; Costanza *et al.* 1997). Costanza *et al.* (1997) estimated the global value of mangrove ecosystem services to be $1,700,000,000 per year, or $9,999 per hectare per year, and they concluded that wetlands are the world's most valuable ecosystems.

1.2 (a) Coastal nutrient cycling

Salt ponds are among the most productive aquatic ecosystems on Earth (Gunter 1967; Mustafa *et al.* 1999; Pinckney *et al.* 1995; Ziegler & Benner 1999). They are likely to play an important, but as yet undescribed, role in the nutrient budgets of mangrove forests. Most studies of nutrient cycling in mangrove habitats have focussed on estuarine mangrove systems in the Pacific and southern Atlantic oceans, where salt ponds are uncommon. These studies show that the exchange of organic matter and nutrients between mangrove forests and marine waters is dependent upon hydrological factors such as the inundation regime and geomorphology (Alongi 1996; Hemminga *et al.* 1994; Kathiresan & Bingham 2001; Lee 1995; Rivera-Monroy *et al.* 1995; Robertson & Phillips 1995; Wolanski 1992). It is generally agreed that mangroves are nutrient sinks and may even import dissolved nitrogen from coastal waters, but at the same time they export particulate nutrients in the form of leaves and other plant parts (Alongi 1996; Dittmar & Lara 2001; Rivera-Monroy *et al.* 1995).

The capacity of mangrove systems to retain and process nutrients is vital to the maintenance of clear coastal waters, on which benthic photosynthesizers such as seagrasses and coral reefs depend (Furukawa *et al.* 1997; Mercer & Hamilton 1984; Morell & Corredor 1993). Salt ponds within mangrove systems should augment this function by retaining and processing runoff waters, which carry land-based nutrients including sewage and agricultural wastes. Nutrients in runoff waters may be effectively absorbed and trapped by the complex microbial communities that occur in many salt ponds (Bebout *et al.* 1994; Des Marais 1995; Javor 1983; Nielsen & Sloth 1994).

Salt ponds also augment the capacity of mangrove systems to capture sediments, which can smother coastal benthic communities in shallow marine waters. MacDonald *et al.* (1997) showed that nearly all of the fine materials running off hillsides in the Virgin Islands collect at the bottom of ravines (locally called ghuts). Where a ghut terminates in a salt pond, sediments carried in runoff water will be retained rather than washed into the sea during heavy rains.

1.2 (b) Salt ponds as wildlife habitats

Salt ponds are a critical resource for resident and migratory waterbirds in the Caribbean. Scott & Carbonell (1986), in their survey of neotropical wetlands, reported thousands of shorebirds at individual ponds throughout the Caribbean islands (e.g. Antigua and Puerto Rico) during migrations. Salt ponds provide abundant food resources and protected roosting and nesting sites for birds (Takekawa *et al.* 2001; Warnock & Takekawa 1995). Salt ponds support nearly all the resident and migratory waterbirds in the BVI due to a lack of comparable freshwater or estuarine habitats. Species such as the endangered West Indian Whistling Duck (*Dendrocygna arborea*) and diving ducks no longer survive in the Virgin Islands because of widespread habitat loss (Norton *et al.* 1986).

1.2 (c) Direct use values

Artemia, used to support the aquaculture and the aquarium industries, are cultured in hypersaline water bodies and may be a viable industry in salt ponds (Goodwin *et al.* 1984). *Dunalliela*, a halophilic unicellular green alga, can also be cultured in salt ponds to produce β-carotenes (used as dietary supplements), glycerol, and as a source of dried protein to feed livestock (Ventosa & Nieto 1995; Williams 1993). Other halophytes have potential in technical industries. For example, bacteriorhodopsin, a photosynthetic pigment in purple membranes of *Halobacterium halobium,* is commercially produced for optical data processing, non-linear optics and as light sensors (Ventosa & Nieto 1995). Halophilic bacteria are also used to produce polyhydroxyalkanoates (PHA), which can replace thermoplastics. Unlike other plastics, PHA is biodegradable, totally resistant to water, and is biocompatible (non-toxic and digestible) (Ventosa & Nieto 1995).

1.2 (d) Indirect use values

1.2 (d.*i*) Ecosystem services

The value of salt ponds in protecting coastal ecosystems by purifying runoff waters, in providing critical habitat for wildlife and as potential economic and scientific resources does not weigh in decision making processes, partly because many people in the BVI view salt ponds as wastelands. Ignorance and misunderstanding of the value of mangrove wetlands has led to their conversion (ambiguously called "land reclamation") for construction or agricultural purposes throughout the Caribbean (Ellison & Farnsworth 1996; Lugo & Snedaker 1974; Mercer & Hamilton 1984). Conversion of wetlands to other uses is a global problem, resulting in a 50% loss of the world's wetlands since 1900 (Michener *et al.* 1997). The future of salt ponds depends heavily on understanding and recognizing their inherent value to human communities, threats to their integrity and the need for ecosystem conservation.

1.2 (d.*ii*) Scientific research

As ecosystems, salt ponds present great potential for scientific research. Physiologists are interested in the nature of biological adaptations to the extreme conditions of hypersaline environments (i.e. high salinity, low oxygen, and intense sunlight). Halophytes in salt ponds present interesting study organisms for biochemists, particularly in their mechanisms for fixing light energy. Even those searching for life on other planets have looked to salt ponds, where some of the most primitive life forms persist because they are protected from most predators and competitors by extreme environmental conditions (Paerl *et al.* 2000).

1.3 The need for an ecosystem study

Caribbean mangrove wetlands that contain salt ponds or salt flats (dry salt pans) are recognized as unique systems, the "basin mangrove forests" (Lugo & Snedaker 1974), which are equivalent to salt pond ecosystems as defined here (Section 1.1). Bacon (1994) showed that more than half of the Eastern Caribbean mangrove wetlands were basin mangrove forests. These ecosystems are being rapidly replaced by coastal developments, and they represent one of the most threatened habitats on Earth (Ellison & Farnsworth 1996; Kathiresan & Bingham 2001; Lewis 1988, 1990; Linden 1990; Macdonald *et al.* 1997; Odum *et al.* 1982; Turner & Lewis 1997). Nevertheless, salt ponds have generally been excluded from ecological studies of mangrove wetlands, and a comprehensive description of hydrological, chemical and biological variation within these systems is urgently needed for the effective conservation and management of Caribbean salt pond ecosystems.

Few studies have addressed the ecology of naturally occurring salt ponds (e.g. Copeland 1967; Kristensen 1964, 1971; Kristensen & Hulsher-Emeis 1972; Lonzarich & Smith 1997). Other studies have described ecological aspects of salterns (e.g. Amaral & Costa 1999; Barbe *et al.* 1990; Britton & Johnson 1987; Carpelan 1957; Davis 1978; Javor 1983; Mustafa *et al.* 1999). Several studies have focused on particular taxa that inhabit hypersaline environments, both inland and coastal, (e.g. Browne & Wanigasekera 2000; Campbell 1995; Caspers 1981; Dexter 1993; 1995; Ginzburg 1987; Herbst 1990; Pejler 1995; Persoone & Sorgeloos 1980; Post *et al.* 1983) of which those addressing benthic microbial communities are most frequent (e.g. Bauld 1981; Blinn 1993; Borowitzka 1981; Des Marais 1995; Javor 1989; Paerl *et al.* 2000; Pinckney *et al.* 1995; van Gemerden 1993).

1.4 Water chemistry and its biological implications

1.4 (a) Salts

Coastal salt pond water is derived from seawater and therefore has similar initial composition (Blinn 1971). Seawater consists mostly of sodium chloride ($NaCl$: 78%), magnesium chloride ($MgCl$: 8.1%), magnesium sulphate ($MgSO_4$: 6.0%), calcium sulphate ($CaSO_4$-$2H_2O$: 4.6%), potassium chloride (KCl: 1.3%), sodium bromide ($NaBr$: 0.78%) and calcium carbonate ($CaCO_3$: 0.34%) (Barbe *et al.* 1990; De Decker & Geddes 1980). Salts, however, begin to crystallize out of solution as evaporation proceeds. Calcite ($CaCO_3$) is the first to precipitate at 2X (two times) seawater concentration, equivalent to a 75 parts per thousand (ppt) concentration of total dissolved solids; gypsum ($CaSO_4$-$2H_2O$) precipitates at 5X seawater (175 ppt); sodium chloride precipitates at 9X seawater (300 ppt) (Barbe *et al.* 1990; Britton & Johnson 1987; Carpelan 1967; Copeland 1967). Thus, while salinity gradually increases by evaporation, the chemical composition of water may change abruptly as ions come out of solution at specific precipitation points.

1.4 (b) Dissolved oxygen

Dissolved oxygen varies inversely with both temperature and salinity, and it follows a diurnal cycle in which water becomes oxygen-depleted by respiratory activities at night and supersaturated by photosynthetic activities during the day (Burke 1995; Burke & Knott 1997; Canfield & Des Marais 1994; Carpelan 1957; Sherwood *et al.* 1991). Due to the declining solubility of oxygen at high salinities and the demand for oxidative respiration, dissolved oxygen concentrations in hypersaline waters may approach zero, particularly at night and at warm temperatures. Consequently, species adapted to high salinity must also be tolerant of low oxygen availability (Bayly 1972; Greenwald & Hurlbert 1993; Gunter 1967).

1.4 (c) Temperature

Daytime temperature in salt ponds may exceed ambient air temperature. This is because the specific heat of water decreases with increasing salinity, causing high salinity water to warm faster than low salinity water. There is also less evaporative cooling at high salinities (Greenwald & Hurlbert 1993). Temperatures in tropical salt ponds may therefore approach 40°C, the limit for eukaryotic production (Burke & Knott 1997; Kristensen & Hulsher-Emeis 1972).

1.4 (d) pH

High pH may limit photosynthetic production because of its effects on the availability of dissolved carbon dioxide. Between salinities of 50 and 70 ppt, pH levels may exceed 9.0 because the concentration of seawater increases the ratio of carbonate to bicarbonate (Carpelan 1957; Copeland 1967). At pH 9 carbon dioxide is no longer available to photosynthetic organisms (Carpelan 1957; Copeland 1967). Some algae and plants can avoid this problem by assimilating HCO_3^- instead of CO_2 (Carpelan 1957; Kantrud 1991). When $CaCO_3$ precipitates at 70-80 ppt, pH drops back to about

8.1 (Carpelan 1957; Copeland 1967). Whether pH co-varies predictably with salinity under natural conditions may depend on hydrological, geological, and ecological factors of the site in question. Meshal (1987), for example, measured pH at 8.1 in water of 51 ppt in a lagoon of the Red Sea, although Carpelan's (1957) pH-salinity model predicts a pH value of 9 for this salinity.

1.4 (e) Inorganic nutrients

Nitrogen and phosphorous are required for cellular function in all organisms. Availability of these inorganic nutrients is often lower than biological demand (Wetzel & Likens 2000). Nutrient concentrations are dynamic because nutrients are utilized, stored, transformed and excreted rapidly and repeatedly by aquatic organisms. Inorganic nutrients concentrate in evaporative environments, and, as a result, salt ponds may have elevated nutrients with respect to seawater (Garcia & Niell 1993). Unlike other salts, concentration of nutrients during evaporative periods may be delayed while they are incorporated into the biotic community (Carpelan 1957). Salt pond waters are also known to be rich in dissolved organic carbon, which is absorbed into the photosynthetic community (Larsen 1980; Nixon 1970).

Garcia-Pichel *et al.* (1999) and Pinckney *et al.* (1995) have suggested that nutrients may exert less control over production than osmotic limitation in hypersaline systems, whereas the opposite is true in more benign environments. However, Davis (1978) showed that fertilization of a Bahamanian saltern stimulated the growth of photosynthetic communities, indicating that these salt ponds were nutrient limited despite their high salinity.

1.4 (f) Effects of extreme conditions on biological communities

Extreme salinities, high insolation, high temperature, low oxygen and seasonal desiccation all contribute to the inhospitability of salt ponds to all but the most widely tolerant aquatic organisms (Bayly 1972; Britton & Johnson 1987; Garcia & Niell 1993; Hammer 1986; Lonzarich & Smith 1997; Williams 1998). The degree to which increasing salinity limits aquatic communities is one of the central questions in the study of hypersaline ecosystems, and salinity is often cited as the most important abiotic force controlling species composition in saline ponds (e.g. Barbe *et al.* 1990; Dexter 1995; Garcia & Niell 1993; Lubzens *et al.* 1985; Persoone & Sorgeloos 1980; Pinckney *et al.* 1995; Woodbury 1942). Salinity tolerance limits have been determined under laboratory conditions for several species, but distinguishing between the direct effects of salinity and the effects of chemical parameters that co-vary with salinity, such as oxygen, temperature, and pH, has proven far more difficult (Garcia-Pichel *et al.* 1999).

1.5 Hypersaline communities

1.5 (a) Limiting factors

The brine shrimp, *Artemia*, which is credited with "the best osmoregulation system known in the animal kingdom" (Persoone & Sorgeloos 1980, pg 13), can survive at salinities below seawater to salinities 10 times higher than seawater concentration (Kirstensen & Hulsher-Emeis 1972), and it can survive in waters with less than 1 part per million (ppm) dissolved oxygen (Persoone & Sorgeloos 1980). Halotolerant and halophilic bacteria and some protists form benthic microbial communities (BMCs) in hypersaline habitats. Functional groups of microbes (cyanobacteria and diatoms, colorless sulfur bacteria, purple sulfur bacteria, and sulfate-reducing bacteria) interact to retain and recycle nutrients and oxygen within BMCs (Des Marais 1995; Pinckney & Paerl 1997; van Gemerden 1993). These interactions may be a key for the survival of BMCs in extreme environments (Paerl *et al.* 2000).

Most aquatic species in salt ponds, however, are unable to survive beyond 100 ppt salinity (e.g. Borowitzka 1981), and species diversity in these systems decreases with increasing salinity (Bayly 1972; Britton & Johnson 1987; Colburn 1988; De Decker & Geddes 1980; Garcia & Niell 1993; Garcia *et al.* 1997; Hammer 1986; Herbst 2001; Lonzarich & Smith 1997; Rushforth & Felix 1982; Timms 1981; Williams 1998; Wolfram *et al.* 1998). Salinity and co-varying chemical and physical conditions, however, may not be the only factors that determine the structure of hypersaline communities. Stochasticity, predation, food availability, competition, other biotic interactions, and interactions between particular physical and chemical factors may also be important (Williams 1998). Understanding the ecological effects of increasing salinity consequently requires community-level studies that incorporate physical, chemical, and biological variation on both spatial and temporal scales (Hart *et al.* 1998).

1.5 (b) Biogeography

Invertebrates inhabiting hypersaline and temporary waters are known to have excellent dispersal abilities (Williams & Kokkin 1988). Several taxa common in hypersaline communities, including *Artemia,* rotifers, and copepods, produce resistant cysts that can be dispersed by birds and even by wind (Lahr *et al.* 1999; Lubzens *et al.* 1985; Persoone & Sorgeloos 1980; Triantaphyllidis 1998; Williams 1985). Aquatic insects can disperse by flight as adults, thereby avoiding rather than resisting periodic extremes of salinity or drying (Lahr *et al.* 1999; Williams 1985). Cole (1968) described hemipterans in East Africa flying as much as 80 km to new ponds. As a result, the known biota of hypersaline communities is widespread (Cole 1968; Hammer 1986; Williams 1998).

Despite the ubiquitous nature of hypersaline taxa, individual pond biotas may be quite variable (Guerrero *et al.* 1994; Javor 1989). Recently, a few investigators have argued that this distribution pattern—wide distribution of individual species but variable representation in similar habitats—suggests the existence of species complexes within those currently grouped as single species (Mielke 2000). Several of the groups in question are notoriously difficult to distinguish, and further systematic work may find a greater diversity of salt pond species than is currently known.

1.6 Goals of this study

This thesis aims to describe the structure, organisation and function of salt pond ecosystems in the British Virgin Islands. It therefore takes a holistic approach, addressing diverse aspects of salt pond ecosystems including biotic composition, chemistry and hydrology with specific reference to both temporal and spatial variation. It is the first of its kind for Caribbean salt ponds, and little complementary data exist from similar systems anywhere in the world.

The data presented here are necessarily descriptive and exploratory and provide a basic understanding of patterns and scales of variation in these systems. The need for such a descriptive study of coastal ponds, encompassing temporal and spatial variation, has been identified by several authors, most recently by Moss (1999).

The extent of biological, chemical, and hydrological variation found in BVI salt ponds could not have been anticipated, and therefore, *a priori* hypotheses would not only have limited the scope of this work but would also have resulted in restraining the researcher from exploring new parameters as their importance became apparent. Orientations for hypothesis-based studies should be viewed as a result, rather than a starting point, of exploratory research in unstudied ecosystems. Consequently, this investigation not only answers several questions about the structure, processes, and dynamics of salt pond ecosystems but also elucidates important new directions for research.

In addition to the general aim of describing salt pond ecosystem characteristics, this investigation specifically addressed the following ecological questions:

- Can shoreline mangrove distributions be used to infer hydrological differences among salt ponds? (Chapter 4)
- What hydrological factors are responsible for salinity variations within and among ponds? (Chapters 4 & 5)
- How do aquatic invertebrate communities respond to changing salinities? (Chapter 6)
- To what extent is the species composition of aquatic communities in salt ponds controlled by geographic habitat separation, by salinity forcing, and by biotic interactions? (Chapter 6)
- How important are BVI salt ponds to waterbird populations? (Chapter 7)
- Should salt ponds be considered as a single habitat type or can distinct subtypes be established and classified? (Chapter 8)

This first chapter has provided a context for the research presented in this thesis. Chapter 2 profiles the study area, discusses the conservation status of its salt ponds and specifically describes each study site. Chapter 3 details the methods employed in this study, and results are presented and discussed in chapters 4 to 9.

Chapter 2: Environmental Profile of the BVI and its Salt Ponds

2.1 BVI profile

2.1 (a) Geography, climate and geology

Geographically, the Virgin Islands form the western extremity of the Lesser Antillean island chain in the eastern Caribbean Sea, but geologically the Virgin Islands belong to the Greater Antilles as they rise from the Puerto Rican shelf, here lying about 65 m below sea level (Martin-Kaye 1959). Most of the Virgin Islands were uplifted from submerged volcanoes, and they are hilly with steep slopes. Tortola, the tallest island, rises to 521 m at Sage Mountain. Anegada, in contrast, is an emergent coral limestone platform with a maximum elevation of 8 m (Martin-Kaye 1959).

The BVI includes about 46 islands and cays located at 18° 30'N and 64° 30'W, 150 km east of Puerto Rico (see Figure 1.1). It has a total land area of 153 km^2, distributed mainly in the 4 largest islands: Tortola (54 km^2), Anegada (38 km^2), Virgin Gorda (21 km^2) and Jost Van Dyke (10 km^2).

These islands are known for their beauty, and their waters are the focus of tourist activities, especially sailing and diving. Approximately 188 km of the BVI's coastline is fringed by coral reefs (http://www.dpu.org), and mangrove wetlands are also abundant. Blok-Meeuwig (1990) measured 587 hectares (ha.) of mangrove forest, distributed among 53 wetland systems in the BVI.

The islands lie within the Trade Wind belt, and the climate is subtropical with a long dry season. Mean temperature ranges from 26 to 31°C in summer and from 22 to 28°C in winter (http://www.caribisles.org). Mean rainfall from 1991 through 2001 was 104 cm/year and ranged from 69 cm in 1994 to 157 cm in 1998, a year that was reported to be rainier than any in at least 25 years (Rowan Roy, pers. comm. 1999). Older BVIslanders describe a generally wetter climate 30 to 40 years ago, and this claim is substantiated by Martin-Kaye's 1959 report of 135 cm mean annual rainfall with extremes of 76 cm and 250 cm between 1901 and (presumably) 1958. Rainfall can vary substantially within 5 km on individual islands (Stoffers 1993), and it can be up to 25% higher on Tortola than on the smaller islands with lower elevation (Goodwin *et al.* 1984; Martin-Kaye 1959). Hurricanes affect the region between July and November. The BVI has experienced 6 hurricanes in the past 10 years.

2.1 (b) Population

The population of the BVI has grown rapidly in response to recent economic growth. The current population of 20,000, 82% of which is concentrated on Tortola, is nearly double that of 1980 (http://www.dpu.org). Eighty percent of the population growth has occurred through immigration (http://www.dpu.org), and BVI citizens constitute only 50.1% of the population (DPU 1994b)

Nearly 400,000 holiday visitors arrive in the BVI each year (BVI Tourist Board, pers. comm. 1999). As a result, the BVI's effective population size, especially during the winter, is far greater than censused population size. Furthermore, a recent turn towards mass cruise ship tourism is raising questions about carrying capacity (Patullo 1996). Tourism development and uncontrolled tourist traffic has had devastating effects in small tropical islands, where tourism is concentrated in coastal areas (Jarecki 1996).

2.1 (c) Territorial history and government

The BVI was first claimed by the Dutch in 1648 but was taken over by English planters in 1666 and annexed by the British in 1672. British settlers emancipated their African slaves in 1838, and people of African descent now comprise 83% of the population (http://www.dpu.org).

A new constitution (1967) provided for a ministerial government, which currently affords the BVI a greater measure of internal self-government than other overseas territories (Jeans 2002). As a British Overseas Territory, a Governor representing HM Queen Elizabeth II is responsible for defence and internal security, external affairs, terms and conditions of service of public officers, and the administration of the courts. All other affairs are the responsibility of the ministerial government.

2.1 (d) Economy

The BVI's economy has evolved over the past 50 years from one that was primarily agricultural to one that encourages tourism and exports financial services (Smith 1996). Tourism, which represents an estimated 45% of the national income, is dependent on the BVI's natural beauty, while financial services, which represent just over 50% of the national income, relies on the BVI's political stability (http://www.geographic.org; http://www.dpu.org). The BVI's historically pristine marine environment inspired the national motto, "Nature's Little Secrets" (inscribed on licence plates) and resulted in the BVI becoming one of the top sailing destinations in the world. Presently, a per capita GDP of $16,000 (purchasing power parity, 2000 est.; http://www.cia.gov) ranks the BVI's standard of living second in the Caribbean basin behind only the Cayman Islands (http://www.smithsgore.com). Approximately 60% of land in the BVI is privately owned and 40% is Crown Land (DPU 1994a).

2.2 Conservation status of salt ponds

Little information currently exists about the status of Caribbean wetlands and particularly of salt ponds (Davidson *et al.* 1999; Scott & Carbonell 1986). Davidson *et al.* (1999), in reviewing wetland inventory information in the neotropics, list only 4 wetlands in the BVI, yet there are nearly 60 salt ponds alone. This lack of information has impeded global and regional wetlands conservation efforts, and it has discouraged local initiatives to conserve valuable coastal habitats. Nevertheless, sewage pollution, erosion and sedimentation are locally recognized as important environmental problems in the BVI. Schumacher *et al.* (1996) showed that tourism-dependent Caribbean communities should have great economic incentive to control land-based marine pollution. Compared with other Caribbean states, the BVI has sufficient economic strength to build the institutional capacity needed to slow the current trend of coastal degradation (Schumacher *et al.* 1996). However, greater political incentive to pay for such capacity building is necessary.

2.2 (a) Threats

2.2 (a.*i*) Loss of habitat

Reclamation is, by far, the greatest threat to the survival of Caribbean mangrove wetlands (Batty 1997; Ellison & Farnsworth 1996; Kathiresan & Bingham 2001; Scott & Carbonell 1986). Economic success and a burgeoning tourist industry in the BVI have driven the construction of hotels, marinas, residences and office buildings in coastal areas.

Figure 2.1 shows the distribution of existing, threatened and historic salt ponds. Historic salt ponds have been completely filled by dredge spoils, excavation spoils and/or solid wastes (Figure 2.2(a,b). They are no longer recognizable as wetlands, and their location has been determined by personal communications with local people (e.g. Bertrand Lettsome, Elvet Meyers and Rowan Roy). Coastal development has, to date, replaced 84% of the number of salt ponds originally on Tortola, and development pressure is now spreading to the smaller outer islands of the BVI, which have thus far experienced 10% salt pond losses (Figure 2.1).

The Conservation and Fisheries Department, an advisory body to the Ministry of Natural Resources, conducted a comprehensive assessment of the major mangrove systems in the BVI in 1990 (http://www.dpu.org). Since this survey, 12 of 17 sites that were identified and accepted by the BVI Government as having critical importance to the BVI have been partially or completely filled. During the course of this doctoral study (1995 – 2002), 5 salt ponds were completely filled (4 on Tortola: Apple Bay Pond, Duff's Bottom Pond, Ross Pond at Cane Garden Bay, Pockwood Pond; 1 on Virgin Gorda: Biras Creek Pond), and 5 others were partially filled (2 on Beef Island: Runway Pond, Trellis Bay Pond; 3 on Tortola: Josiah's Bay Pond, Brandywine Bay Pond, Witches Brew Pond).

2.2 (a.*ii*) Erosion

Accelerated sedimentation represents a significant indirect threat to salt pond ecosystems (Lewis 1988; MacDonald *et al.* 1997). Construction on hillsides loosens and exposes soils that are carried by runoff water into salt ponds and bays (Figure 2.2(c). MacDonald *et al.* (1997) showed that road erosion, in particular, has caused at least a 4-fold increase in sediment yields on St. John USVI since the 1950's. These authors determined that each kilometre of unpaved road produces nearly 40 tons of sediment per year, most of which is deposited in salt ponds or in shallow marine waters. The sediment loads to which salt ponds, seagrass beds and coral reefs are currently being subjected are unprecedented (MacDonald *et al.* 1997) and should be regarded as a serious threat to coastal biodiversity in the Caribbean.

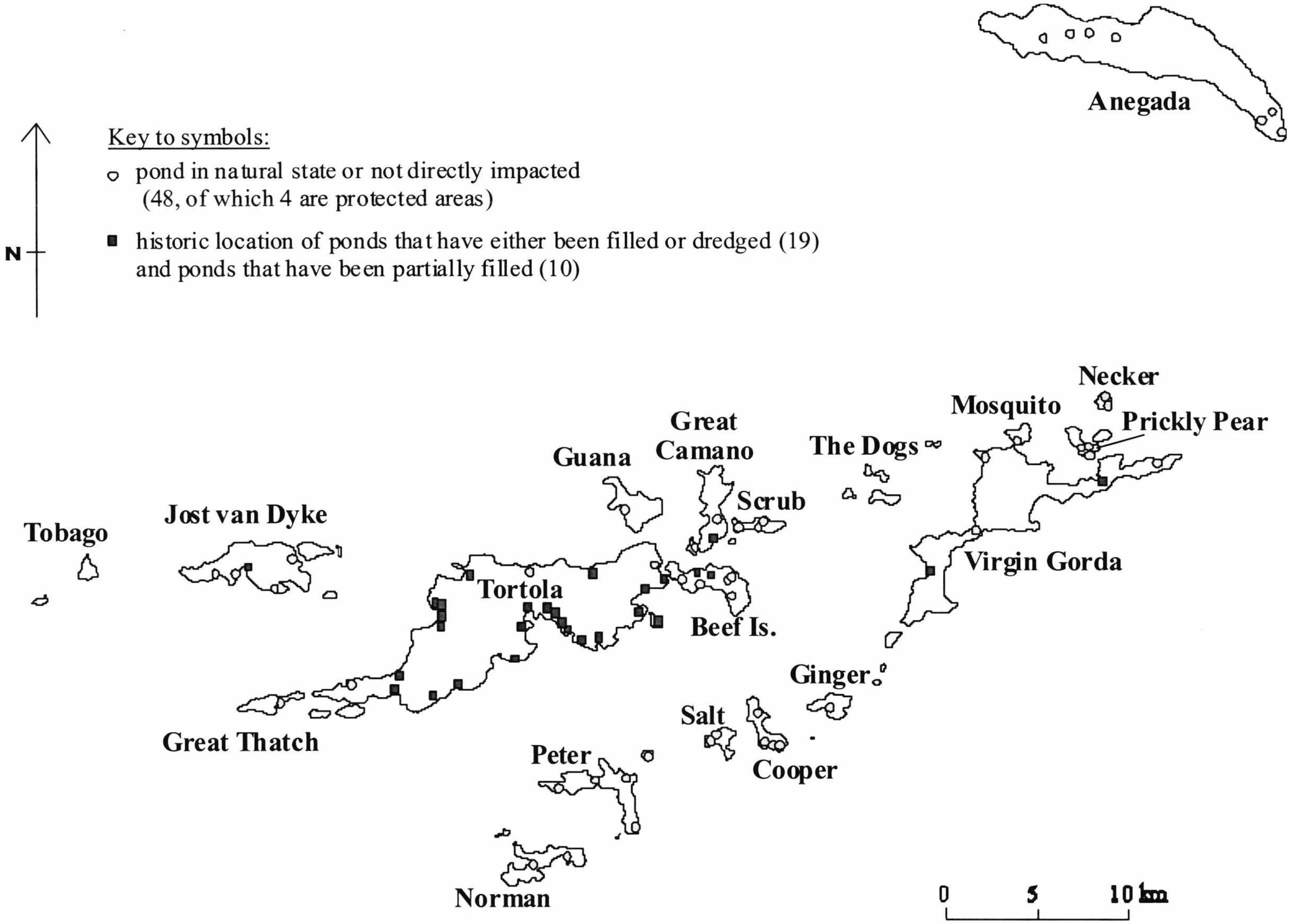


Figure 2.1 Geographic distribution and status of salt ponds

2.2 (a.*iii*) Sewage

Sewage from leaking septic tanks and from discharge pipes is also carried to the coast in runoff waters. Schumacher *et al.* 1996 argued that sewage pollution is the most serious and widespread pollution problem in the Caribbean. Sewage effluent in mangrove areas such as salt ponds may be sequestered and processed by sediment bacteria, but processing efficiency tends to decrease with increasing input because high organic loads shift balanced aerobic-anaerobic systems to complete anaerobiosis (Robertson & Phillips 1995). Additionally, toxic elements in wastewater accumulate by evaporation in salt ponds. Tanner *et al.* (1999) reports annual bird kills in the Salton Sea due to bioaccumulation of toxic elements in water draining from agricultural lands.

a) Construction fill in Brandywine Bay Pond, Tortola, 2002

b) Solid waste in Witches Brew Pond, Tortola, 1995

c) Road construction without erosion control, above Witches Brew, Tortola, 2002. Such practices accelerate sediment deposition in salt ponds

d) Results of a fuel spill in Pockwood Pond, Tortola, 2000
(photo by Bruce Potter)

Figure 2.2 Filling, dumping and other impacts on BVI salt ponds

Only one municipal sewage treatment facility currently exists in the BVI, and it services approximately 70 buildings constructed along the shoreline at Cane Garden Bay, Tortola. Most buildings outside of the capital (which pumps sewage to an outfall) use septic tanks and soakaways for sewage disposal. Soakaways do not adequately contain sewage flow because of the BVI's thin soil layer and impermeable bedrock (Howard Watson, pers. comm. 2002). Salt ponds capture runoff that flows through soakaways, and their natural ability to filter and purify runoff waters should be a focus of non-point source pollution concerns. Sewage overload in salt ponds has been reported from other Caribbean islands (Scott & Carbonell 1986), and rapidly expanding hillside housing developments may ultimately cause such problems within BVI salt ponds as well.

2.2 (a.*iv*) Oil and other petroleum products

Oil pollution in mangrove wetlands has been reported from several Caribbean islands (Scott & Carbonell 1986). Oil can smother and kill vertebrates and invertebrates alike, and it is toxic to mangrove trees (Kathiresan & Bingham 2001). Oil spills at sea tend to affect the shoreline fringe of red mangrove rather than salt pond communities. Several activities, however, introduce petroleum directly into salt ponds.

In the BVI, waste oil from cars is frequently disposed of into the ground, or even sprayed on dirt roads to control dust. Leaks in underground fuel tanks are generally not identified until fuel begins leaching into coastal waters (Figure 2.2 (d)). Rain can wash discarded or leaked petroleum through the soil and into ponds. Furthermore, diesel fuel is used to control mosquitoes in mangrove and salt pond habitats. The BVI Environmental Health Department has a mosquito control program in which its employees regularly pour into salt ponds a mix of diesel and "malaria oil", a light oil marketed to control mosquitoes in water bodies (Minchie Israel, pers. comm. 2000). This forms an oil slick across the surface of the water and suffocates mosquito larvae before the diesel and oil evaporate. This practise also kills other air-breathing insects such as corixids, and introduces toxic compounds into the ecosystem. Masses of dead corixids have been observed on the shores of ponds after treatment, and several successive treatments have caused mangrove defoliation (Aragorn Dick-Reed, pers. comm. 1999). This study determined that high salinity and insolation generally prevent mosquitoes from using salt ponds for reproduction. In light of these results, the Environmental Health Department now restricts their treatments to small, shaded ponds, which are first tested for the presence of mosquito larvae (Minchie Israel, pers. comm. 2001).

2.2 (a.*v*) Global climate change

Mangrove ecosystems are not only threatened by local land use and pollution problems but also by the globally accelerated rise in sea level, caused by the thermal expansion of the oceans and melting of ice caps and glaciers in response to global warming (Ellison 1994, 1996; Kathiresan & Bingham 2001; Michener *et al.* 1997). Bacon (1994), however, refuted the idea that major mangrove ecosystem changes will result from predicted sea level rise, and he concludes that mangroves and salt ponds will, in fact, expand as inundation moves landward. While such expansion may occur in some areas, human encroachment has undoubtedly restricted the ability of mangroves to respond to environmental changes such as sea level rise (Batty 1997; Ellison & Farnsworth 1996; Michener *et al.* 1997; Wolanski & Chappell 1996).

Models of global warming also predict increasing frequency and intensity of hurricanes in the Caribbean (Ellison 1994; Michener *et al.* 1997; Paerl *et al.* 2003). Hurricanes can have substantial impacts on coastal wetlands. Tabb & Jones (1962) detail the effects of Hurricane Donna in North Florida Bay. Winds of 240 km/h destroyed mangrove trees in some areas, and the bottoms of shallow bays and ponds were scoured by storm tides, which extended 14 to 19 km inland. Churning of sediments released toxic hydrogen sulphide into the water column. Fish and marine invertebrates were carried inland and stranded in shallow ponds in which sediments were suspended, hydrogen sulphide concentrations were high, and dissolved oxygen was depleted due mainly to the decomposition of mangrove leaves. Changes in the frequency and intensity of hurricanes are expected to have substantial impacts on coastal wetland patterns and processes (Michener *et al.* 1997). Paerl *et al.* (2003), however, showed that pulses of freshwater brought by tropical storms can enhance BMC productivity, carbon dioxide sequestration and nutrient cycles in salt ponds.

2.2 (b) Protection

2.2 (b.*i*) Development control

The Land Development Control Ordinance (1979) assigns responsibility for the formulation, evaluation and management of all development plans whether public or private, to the Development Control Authority, whose members are appointed by the

Governor. Recently, however, an advisory body known as the Planning Review Committee, which is chaired by the Chief Minister, has taken over the task of reviewing development applications. This committee is an inter-ministerial body that is intended to represent a variety of stakeholder interests, but conservation and natural resources interests are rarely represented (Jeans 2002). As a result, decisions have often reflected short-term economic or political goals rather than sound development practices. In June 2003, however, a new party was elected to government, and it is expected that environmental issues will be given a higher priority.

Environmental impact assessments (EIA) are required by the Virgin Islands Planning Act (1998) "unless the Authority otherwise determines". The Act does not discuss the situations in which the Authority may determine otherwise, and this clause effectively undermines the requirement for environmental impact assessments. The general perception among developers and community leaders is that an EIA is not required unless specifically stated for individual development projects (Jeans 2002).

In response to demands from the United Kingdom, the BVI Chief Minister signed an Environmental Charter in September 2001 (www.ukotcf.org/OTcharters). This Charter represents an agreement between the BVI and the UK and lays out 10 guiding principles, including the following particularly proactive ones:

- To identify environmental opportunities, costs and risks in all policies and strategies.
- To seek expert advice and consult openly with interested parties on decisions affecting the environment.
- To aim for solutions which benefit both the environment and development.
- To safeguard and restore native species, habitats and landscape features, and control or eradicate invasive species.
- To control pollution, with the polluter paying for prevention or remediation.

These principles offer concrete solutions to threats faced by coastal habitats, but successful implementation of the Environmental Charter will require a massive shift in political priorities and public perceptions.

2.2 (b.*ii*) Regional agreements

The BVI is signatory to at least two regional agreements that obligate participants to protect coastal ecosystems. The Convention for the Protection and Development of the

Marine Environment of the Wider Caribbean (Cartegena Convention 1983) was ratified by the BVI in 1986 and entered into force in 1987 (Jeans 2002). As party to the Convention, the BVI is legally bound to protect and preserve rare or fragile ecosystems, as well as habitat of threatened species. This agreement was furthered by the Protocol Concerning Specially Protected Areas and Wildlife in the Wider Caribbean Region (SPAW Protocol), which was ratified by the BVI in 1990 (Jeans 2002). The Protocol Concerning Pollution from Land-Based Sources and Activities (LBS Protocol), which addresses sewage and sediment runoff, has not been adopted by the BVI due to a lack of infrastructure (Jeans 2002).

More recently (2001), the BVI signed the St. George's Declaration of Principles for Environmental Sustainability in the OECS (Organisation of Eastern Caribbean States). This declaration sets guidelines for integrating social, economic and environmental concerns in national development policies, improving legal and institutional frameworks, ensuring meaningful participation by civil society and the private sector in decision making and management practices, using economic instruments for environmental management, addressing the causes and impacts of climate change, controlling and managing waste, ensuring the sustainable use of natural resources, protecting natural heritage and biodiversity, promoting cooperation in science and technology, and other practices for ensuring environmental sustainability.

2.2 (b.*iii*) International agreements

The BVI is also signatory to 4 international conventions that require members to protect coastal wetlands and the wildlife they support.

The 1995 Jakarta Mandate recommends integrated marine and coastal management for promoting the sustainable use of biological diversity. To meet the need for integrated coastal zone management, the BVI must fortify environmental legislation for the protection of the coastal zone and strengthen institutional capacity for implementation (Jeans 2002).

The Convention on Biological Diversity (CBD) requires contracting parties to promote ecosystem protection and the recovery of threatened species. The Bonn Convention provides a mechanism for developing international agreements that seek to manage populations of endangered, threatened and declining migratory species. The BVI has indicated its intent to implement measures required under the Bonn Convention and the

Convention on Biological Diversity, but the timetable originally presented has not been met, primarily because of insufficient local environmental legislation and enforcement capacity (Jeans 2002).

The BVI joined the Ramsar Convention in 1999, when the western salt ponds of Anegada were awarded recognition as a wetland of international importance (Ramsar Site #983, November, 1999; www.ramsar.org/w.n./europe_sites.htm). The Convention requires that member states "ensure the wise use and conservation of wetlands" throughout their territory (Davis 1994, pg. 9). It specifically requires the inclusion of wetland conservation considerations within national land-use planning, the promotion of wetland conservation beyond the designated Ramsar site and strict protection measures for wetland reserves of small size or particular sensitivity (Davis 1994). All BVI salt ponds fit these criteria for strict protection. As a member of the Ramsar Convention, the BVI is obligated to protect salt ponds, and yet the government currently has no legal means of doing so.

2.3 Description of study sites

Twenty-one ponds throughout the BVI were sampled at least once during this study. Some of the largest as well as smallest ponds are represented, and several, though nearly pristine at the onset of this study (1995), are currently under severe threat by development activities. The 17 most frequently sampled ponds are listed in Table 2.1 with abbreviated names that are used throughout this thesis.

2.3 (a) Anegada

The western ponds of Anegada form a vast interconnected system that joins the sea through a narrow channel at the southern end of Pt. Peter (Figure 2.4). This system forms one of the largest remaining mangrove wetlands in the Lesser Antilles (Scott & Carbonell 1986). The importance of Flamingo Pond, the largest of the Anegada ponds, was recognized in 1977 with the establishment of the Flamingo Pond Bird Sanctuary, though this status merely prevents bird hunting (Jeans 2002). The ponds are in nearly pristine condition, though years of grazing by feral animals have damaged the surrounding vegetation (Downs 1997; Mitchell 1999).

Table 2.1 Key to abbreviated pond names

Abbreviation	Pond name	Location
BAN	Banana Wharf Pond	Beef Island
BEL	Belmont Pond	Tortola
BLU	Bluff Bay Pond	Beef Island
BON	Bones Bight Pond	Anegada
FLA	Flamingo Pond	Anegada
GUA	Guana Island Pond	Guana Island
HAN	Hans Creek Pond	Beef Island
JOS	Josiah's Bay Pond	Tortola
LEE	Lee Bay Pond	Great Camanoe
LON	Long Bay Pond	Beef Island
NOR	Norman Island Pond	Norman Island
PTP	Point Peter Pond	Anegada
RED	Red Pond	Anegada
RUN	Runway Pond	Beef Island
SAL	Salt Island Pond	Salt Island
SIN	Sinky Pond	Tortola
WB	Witches Brew Pond	Tortola

A growing population of re-introduced Greater Flamingos (Lazell 2002) has become a major attraction for tourists (Tony Smith, pers. comm. 2003). As tourism development on Anegada begins to encroach upon the salt ponds, the BVI National Parks Trust is negotiating boundaries for a national park with the people of Anegada, who ultimately control land use on the island (Downs 1997). The proposed park includes both the western and eastern salt ponds.

Anegada is currently under severe threat due to its great potential for tourism and a locally acute need for economic opportunities. Unspecified land ownership on Anegada in general (IRF 1977) has confounded efforts towards development planning and habitat conservation. Despite the designation of its largely pristine western salt pond system as the BVI's only Ramsar site, its most important wetland and a proposed national park, roads are currently being cut into and along Anegada's salt ponds (Figure

2.3). There appears to be no possibility for regulation of land-use activities within the Ramsar site until the long-standing plan to award Anegada's residents title to their lands and to award the BVI National Parks Trust title to the western salt pond complex is implemented by the BVI government (Nancy Woodfield, pers. comm. 2003).

Figure 2.3 Land clearing at FLA, within the Anegada salt ponds Ramsar site, 21 April 2003

Bones Bight Pond (BON, 57 ha.) lies at the northern end of the system (Figure 2.4). A short channel at the southeastern corner of BON leads to Manhead Pond, a small central pond that connects with Point Peter Pond (PTP, 72 ha.) at its southern end. Flamingo Pond (FLA, 220 ha.) forms the southwestern portion of the system. A long channel at its southeastern end leads to PTP. Red Pond (RED, 110 ha.) is the most isolated and lies at the northwest corner of the system. A sand bar occasionally isolated RED from the channel during late winter and early spring, when sea level is lowest (Rondell Smith, pers. comm. 1999). A long channel at its southern end leads to PTP. Budrock Pond is not part of the western pond system but lies in the remote and inaccessible eastern part of Anegada.

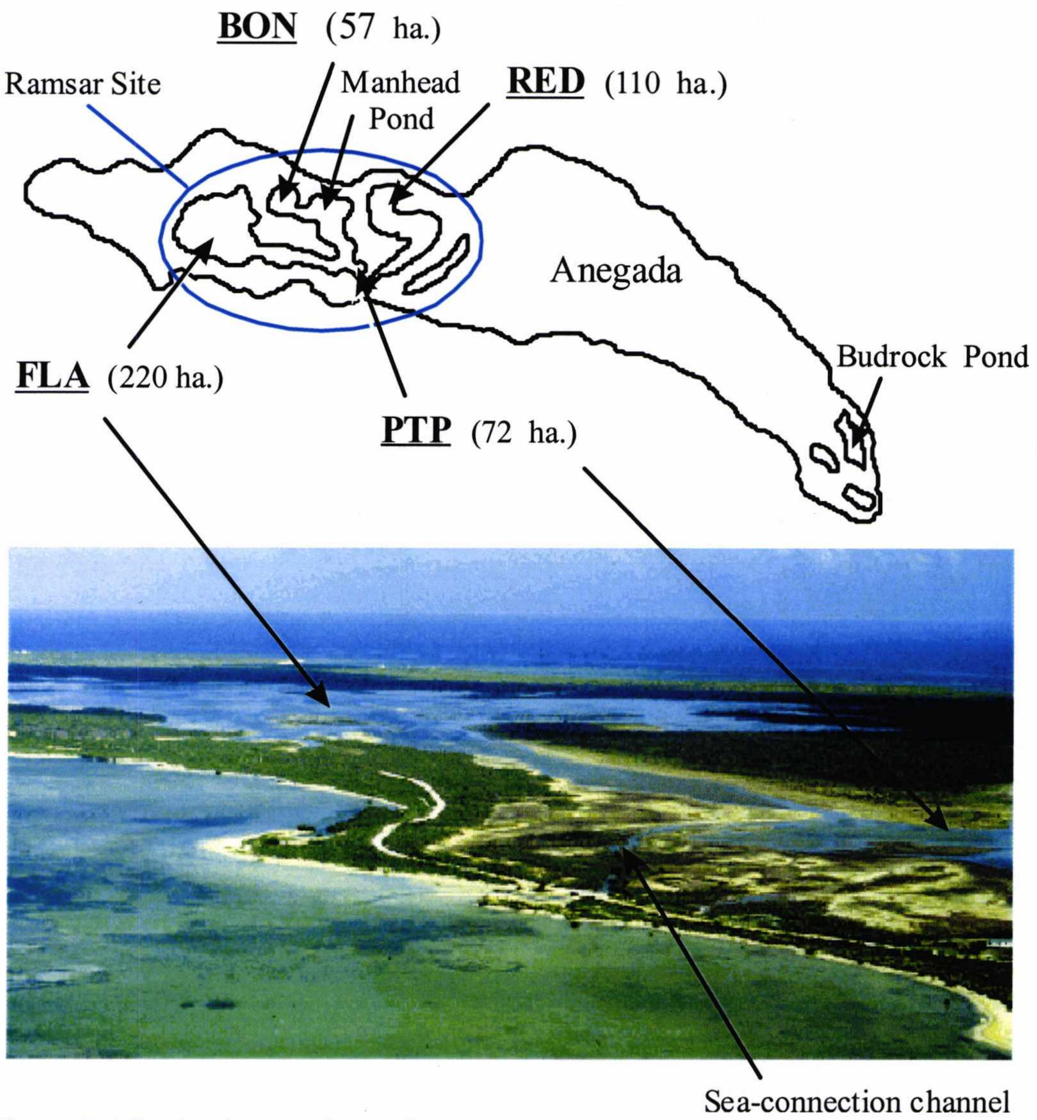


Figure 2.4 Study sites on Anegada

2.3 (b) Beef Island

Banana Wharf Pond

Banana Wharf Pond (BAN, 3.0 ha.) is a completely enclosed, permanently inundated pond located on the north side of Beef Island, just east of Trellis Bay and Sprat Point (Figure 2.5). The historical meaning of its name appears to be lost, but a time when the pond was used as a hurricane shelter for traditional shallow-keeled boats is remembered by some of the oldest residents (Oscar Chalwell, pers. comm. 1991). A forested berm composed of large coral rubble separates the pond from the sea at its northern side; all other sides border hills. The ruins of a lime kiln on the pond's southern side suggests that coral rubble collected from the berm was once transported across the pond and burned to produce lime for construction (Michael Kent, pers. comm. 2000).

BAN is in pristine condition, and its remote location and difficult access have protected this pond from the effects of development. It is, however, privately owned, and current development plans include replacing nearby mangrove forests with a golf course and vacation villas (OBM 1996).

Bluff Bay Pond

Bluff Bay Pond (BLU, 3.6 ha.) is a completely enclosed pond that dries seasonally. It is located on the southern side of Beef Island, behind a sand berm at Bluff Bay (Figure 2.5). Development activities have not yet reached its remote location but in 1999 the pond was surveyed for a planned dredging operation to create a marina. These plans appear to have been abandoned.

Central Beef Island Salt Flats

Lying behind the beach at the eastern end of Trellis Bay, several salt flats occur within a large mangrove wetland. This area is inundated during rainy periods. According to the Trellis Bay Development Plan (OBM 1994), a golf course is scheduled to replace this wetland.

Hans Creek Pond

Hans Creek Pond (HAN, 0.4 ha.) lies at the southern side of Beef Island. It is essentially a salt flat, inundated only after rainfall. Massive land clearing for an airport expansion project, begun in 2001, has greatly accelerated sedimentation in this pond, and terriginous soil has accumulated over the original sandy sediments (Figure 2.5). This pond borders a highly productive mangrove and seagrass lagoon that has been identified as one of the most productive fish nursery areas, particularly for commercially fished species, in the entire BVI (Munro & Watson 1999).

Long Bay Pond

Long Bay Pond (LON, 8.6 ha.), also called Goose Hole Pond (Goodwin *et al.*1984) is located between Long Bay Beach and Goose Hole (Figure 2.5). A road along the southern shore of Beef Island defines its southern boundary. Three culverts under the road allow seasonal sea connection during high tidal cycles. An elevated road to Long Bay Beach was built across the pond's eastern end in 1999.

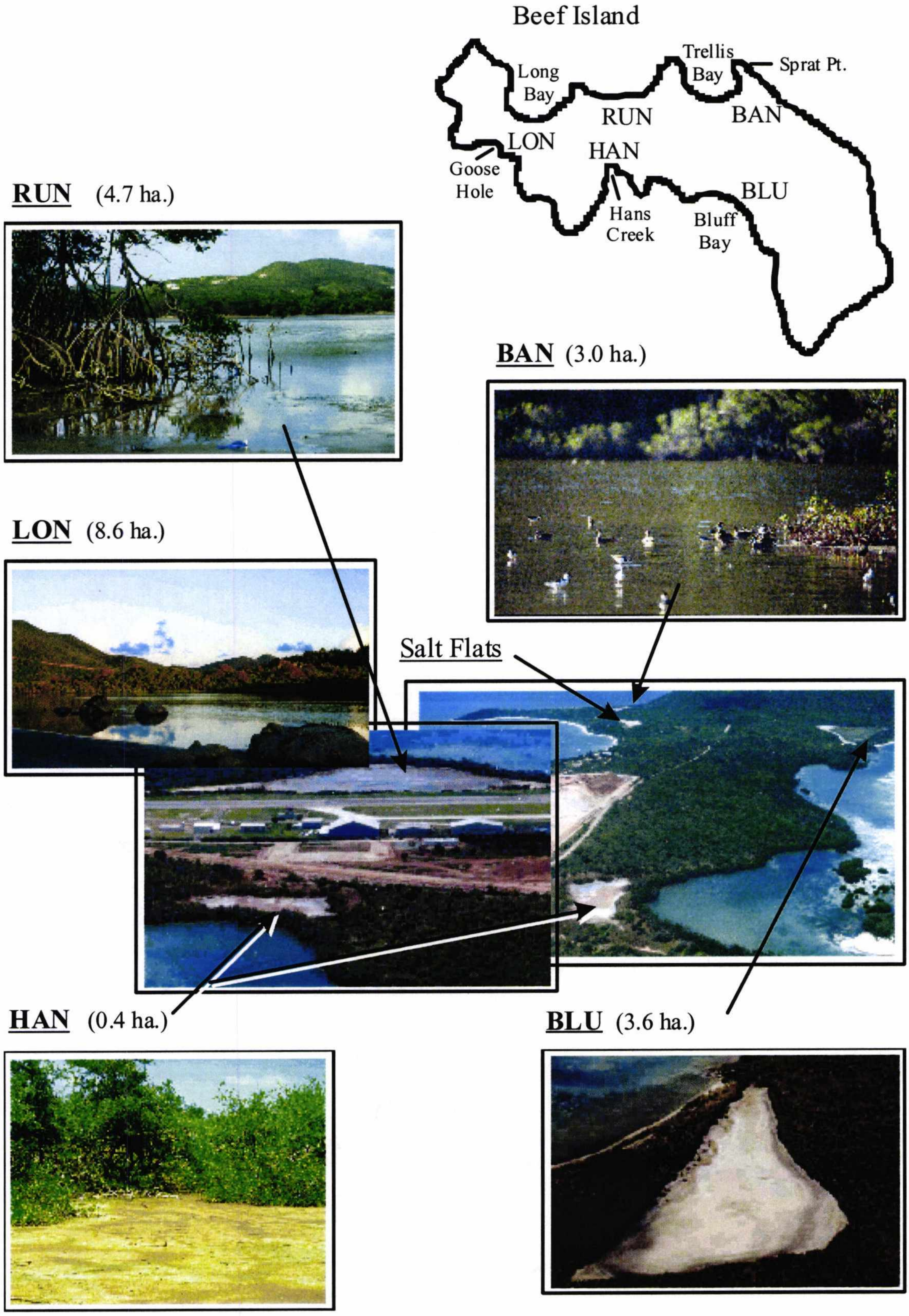


Figure 2.5 Study sites on Beef Island

Runway Pond

Runway Pond (RUN, 4.7 ha.) is a completely enclosed pond that dries seasonally. It lies adjacent to the airplane runway on the north side of Beef Island (Figure 2.5). The airport expansion project required partial filling of the pond and clearing of its fringing mangroves. A security fence around the airport now encloses the pond, making it inaccessible.

2.3 (c) Tortola

Belmont Pond

Belmont Pond (BEL, 13 ha.) is a permanently inundated pond at the west end of Tortola (Figure 2.7). It is separated from the sea at Smuggler's Cove, its western border, by a coral and sand berm high enough to support dry forest vegetation. A lower berm at the pond's north end encloses the pond near Long Bay. A seawater seep feeds the pond at the lowest point of this berm. There is also a coral wall, approximately 50 m long that exists near the seep. The historical significance of this wall is unknown.

BEL, once targeted as a site for marina construction (Insular Environments 1985), is currently being considered for national park status. It is located behind a popular tourist beach, and housing developments are multiplying on the adjacent hillsides. The archaeological remains of a Taino Indian village were recently discovered at the eastern end of BEL (Peter Drewet, pers. comm. 2000). These artefacts and the wetland's natural beauty speak for its inherent value to the BVI community.

Josiah's Bay Pond

Josiah's Bay Pond (JOS, 9.0 ha.) is a fully enclosed pond on Tortola's north shore (Figure 2.7). Parts of JOS are currently (2003) being reclaimed (Figure 2.6) by private landholders, each of whom holds title to a section of the pond that is included in the landholder's registered parcel.

Before recent filling activities, a channel (*ca.*150 m long) ran from the main pond towards the sea but was blocked by a sand berm that formed the upper beach at Josiah's Bay. This berm was sometimes broken through when very heavy rains flooded the pond. After such an event, the sea connection was maintained for a short while (days to weeks) before waves rebuilt the berm by depositing sand in the channel and on the beach. Opportunistic fishermen captured shrimp, crabs and fish that entered JOS during these periods of sea connection. Local residents report that the channel was also dug out by hand in years when it did not break through naturally. Opening of JOS to the sea has not occurred since 1995.

Figure 2.6 Filling of JOS, 28 December 2002

Sinky Pond

Sinky Pond (SIN, 1.5 ha.) is a permanently inundated pond at the northern point (Cannon Point) of Cane Garden Bay. It is also called Fresh Pond and is known for its low salinity relative to other ponds. Once larger, its entire eastern end was used as a waste dump and then filled in the late 1980's (Goodwin *et al.* 1984), and this area now serves as a dry dock.

Witches Brew Pond

Witches Brew (WB, 1.8 ha.) is a complex of ponds connected by wide channels within a larger mangrove forest (Figure 2.7). It is seasonally connected with the lagoon at Bar Bay through a depression in the berm that is breached during high tidal cycles. These events offer fishermen easy access to fish and crabs washed in during tidal floods. The pond is permanently separated from the sea by a wide, forested sand berm on its eastern side.

Historical solid waste disposal in parts of the northwestern shore remains evident today, nevertheless, much of the pond is untouched. Donation of the Witches Brew wetland to the National Parks Trust has been in negotiation for several years, yet a portion of its mangrove forest was filled during the latter part of 2002.

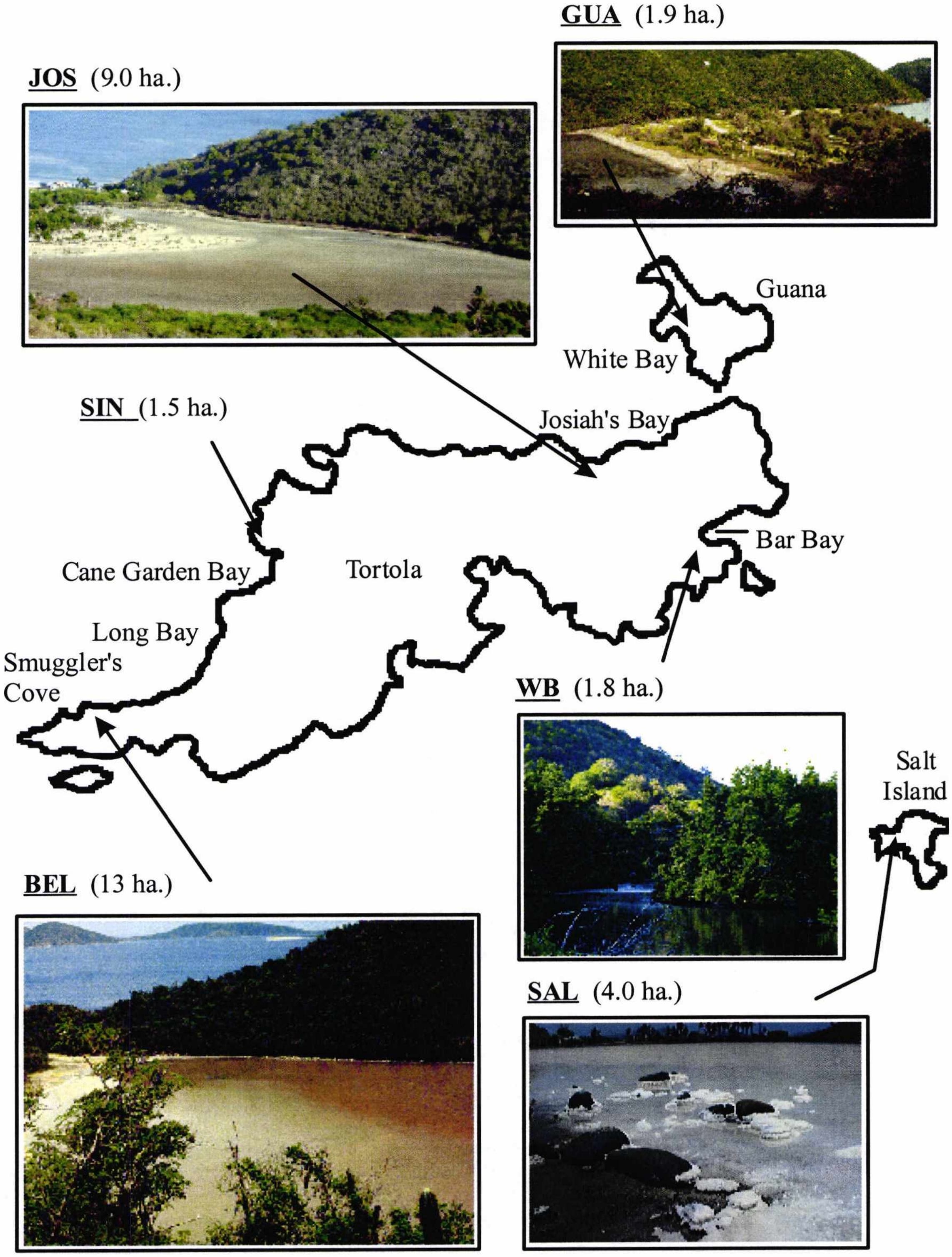


Figure 2.7 Study sites on Tortola, Guana Island and Salt Island

2.3 (d) Small outer islands

Great Harbour Pond

Great Harbour Pond has been reduced by filling to a small, channelised wetland that floods after rainfall or during high tides when a drainage ditch creates a temporary connection with the sea. This pond sits at about the middle of Jost Van Dyke, behind a sand berm at the main harbour (Great Harbour).

Great Thatch Pond

A pond lies at a narrow point in the landmass of Great Thatch Island, which is uninhabited. The pond is completely enclosed and is probably also permanently inundated, though this remains unconfirmed. A narrow berm composed of coral and sand creates the pond's southern shore, while another wider and forested berm occurs at its northern side.

Guana Island Pond

One pond (GUA, 1.9 ha.) exists on Guana Island. It is completely enclosed, and it is separated from the sea at White Bay by a wide (180 m), forested sand berm (Figure 2.7). The pond sits within a privately managed wildlife sanctuary.

A desalination plant, serving the freshwater needs of the island's hotel, was installed near the pond in 1990. Seawater overflow and hypersaline effluents from the desalination plant were directed into the pond. Around the same time, 8 flamingos were introduced to the pond as part of a pilot study for a larger species re-introduction project, which eventually took place on Anegada. The constant input of effluents changed the pond from one that dried seasonally to one that was permanently inundated, which was deemed more desirable for flamingos. Today, the pond remains in this semi-natural state and is managed for the benefit of flamingos and other waterbirds.

Lee Bay Pond

A small temporary pond (LEE, 0.32 ha.) lies at an isthmus in the land on Great Camanoe. Once privately owned, it was donated to the National Parks Trust in 1999, and it now enjoys full protection as a national park. Little development has occurred around the pond or in its watershed.

Norman Island Pond

A small temporary pond (NOR, 0.42 ha.) sits at about the middle of the island, behind a sand berm deep inside the main harbour (The Bight) at Norman Island. A beach bar was built on the berm in 1998, and for 3 years sewage and other wastewater ran into an open pit adjacent to the pond. A proper septic system was installed in 2002 after ownership changed.

Salt Island Pond

Two ponds exist on Salt Island. The one included in this study (SAL, 4.0 ha., Figure 2.7) lies just behind the nearly-abandoned settlement on Salt Island, and the other lies to the west of this pond. A seawater seep trickles into SAL through a berm on SAL's southern shore. SAL's natural ability to produce salt stimulated a thriving salt industry earlier this century and gave this pond historical significance (Colli 1988). The island was leased to its inhabitants for an annual rent of 2 bags of salt, which is still occasionally collected by the territorial governor (Narwel Durant, pers. comm.).

Sandy Cay Pond

A mangrove wetland (SAN) makes up about 1/4 of the land area on Sandy Cay, just off the southeast end of Jost Van Dyke. Most of the wetland is a mangrove forest, but a small salt flat occurs near the centre of the island.

This island is privately owned and protected from development activities. Negotiations are currently underway to transfer ownership to the BVI National Parks Trust with strict requirements for active management and protection of its forest.

This chapter provided an overview of the BVI and the status of wetland conservation in this territory. The salt ponds sampled during this study were specifically described. In the following chapter, methods used to investigate salt pond ecology are presented.

Chapter 3: Methods

3.1 Introduction

For this thesis, I necessarily took an empirical approach to investigating salt pond ecosystems because my goal was to evaluate broad patterns of variation across a wide range of parameters in an unknown ecosystem.

Study sites were selected to include a full range of ponds in their natural states, though accessibility was also an important criterion. After preliminary sampling during the summers of 1991 to 1994, a territory-wide survey of salt ponds was conducted. Ten ponds distributed across 5 islands were identified as appropriate study sites, and a number of ecological parameters that are routinely used for water quality and ecosystem assessment were monitored monthly in these ponds throughout 1995. Monitored parameters included water chemistry, vertebrate and invertebrate abundances, and photosynthetic community characteristics.

The 1995 monitoring work led to a general description of salt pond ecosystems and thus fulfilled a major goal of this study. It also revealed high variability among ponds in several chemical and biological parameters, which commanded further inquiry. Subsequent investigations, performed between 1998 and 2001, were aimed at answering the following 2 questions:

1. How is salinity variation linked to hydrological variation in ponds?
2. What factors control the observed variation in zooplankton distributions?

Sampling during the latter years of this study was less regular but more intensive than during 1995. It focussed on hydrological and chemical parameters, but collection of biological data continued. Additional ponds were included with the original list of 10 sampling sites if they exhibited unique hydrological characteristics or, due to their proximity to one another, allowed intensive sampling among different ponds within a small area. In all 21 ponds were included in ecological and/or hydrological analyses.

The resulting data, while successful in illustrating variation across ponds for each parameter, contained gaps where parameters were measured in some ponds but not in others. Differences in the number of chemical and biological data points among ponds also resulted from changes in the subset of sampling sites. Analyses that compared biological data with chemical data therefore included only those samples in which both sets of values were measured, whereas descriptions of overall chemical characteristics included all relevant data points. Standard deviations are used throughout this thesis to describe variation among groups of data points.

Salinity was used as the primary environmental parameter despite that co-varying effects of low oxygen, high temperature, and high pH in combination with high salinity may impose more stringent physiological limitations on the biota of salt ponds than any one of these factors alone. The advantage of using salinity as an environmental indicator is that it does not fluctuate substantially on a diurnal basis, that it is simple to measure, and that it is an important limiting factor in its own right. It is also the descriptor traditionally used to describe saline water bodies.

3.2. Hydrological analysis

3.2 (a) Pond and watershed dimensions

The British Virgin Islands National GIS database (2001-2002), provided by the Conservation and Fisheries Department with assistance by Alan Mills, was used to calculate the area, perimeter and nearest distance to the sea for each pond (see Table 4.1). These dimensions included only the regularly inundated, non-vegetated portion of each pond.

Watersheds were measured by tracing the approximate area of hillside that drained into each pond over a GIS contour map. Pond areas were included in watershed dimensions (see Table 4.1). Contours for Anegada, Norman Island, and Sandy Cay were not available, and figures for the latter 2 were not estimated. The watershed areas for Anegada, which is flat (maximum elevation 8 m), were estimated as 1 ½ times the area of each pond. Watershed area was used as a relative measure of the potential effect of rainwater entering each pond.

3.2 (b) Duration of inundation and pond depth

Pond inundation (presence or absence of standing water) was noted during site visits and at any other time when such observations were possible (e.g. travelling within view of a pond). Residents living or working near each pond were also asked to estimate the portion of a year that a pond was normally inundated. These estimates were used to evaluate whether the measured inundation periods were typical. Inundation periods are reported as the number of months per year that each pond was continuously inundated (see Table 4.1).

Water depth was measured using a weighted measuring tape at permanent sampling stations at each of 10 ponds during 1995 only (see Section 4.2 (a) and Figure 4.1).

3.2 (c) Geomorphology and connection with the sea

Observations of geomorphology, surface connection with the sea, berm structure, sediments, and surrounding land use were noted while walking the perimeter of each pond. Dimensions of the channel that leads from the western Anegada pond system to the sea were measured with a 50 m transect tape. Water flow in this channel was measured at mid-tide, 7 am, 22 April, 2000, when tidal flow out of the ponds was near its peak (see Section 4.2 (a.*v*)). A piece of wood that floated just under the water surface was placed in the channel about 5 m upstream from the channel's narrowest point. Current flow was calculated from the time required for this wood to travel 10 m downstream.

3.2 (d) Tidal influence

Diurnal water level fluctuations were measured in 13 ponds during the years 2000 and 2001 (see Table 4.2 and Figures 4.3 – 4.6). A small marker was placed into the shore mud at the initial water line, and the distance along the shore from the initial marker to the new water line was measured after several hours. Measurements were taken 3 to 5 times through full tidal cycles. The distance that the water line travelled up or down the shoreline was converted to vertical depth change by triangulation using the slope of the shore as diagrammed in Figure 3.1.

To determine the shore slope at the measurement area, a 31 cm wooden ruler was laid upon the shore, orientated parallel to the slope. A second, shorter ruler was pushed vertically into the ground at the down-slope end of the wooden ruler. A spirit level was placed on top of the wooden ruler, and the lower end of the wooden ruler was raised until horizontal, as indicated by the spirit level. The raised distance was measured from the vertical ruler as the distance between the shore surface and the position of the horizontal ruler. The raised distance (h) was divided by the length of the wooden ruler (31 cm = x) to give the sine of angle a ($\sin a$), as shown in Figure 3.1. Each measured distance between water levels (D) was multiplied by $\sin a$ to give the vertical change in pond depth.

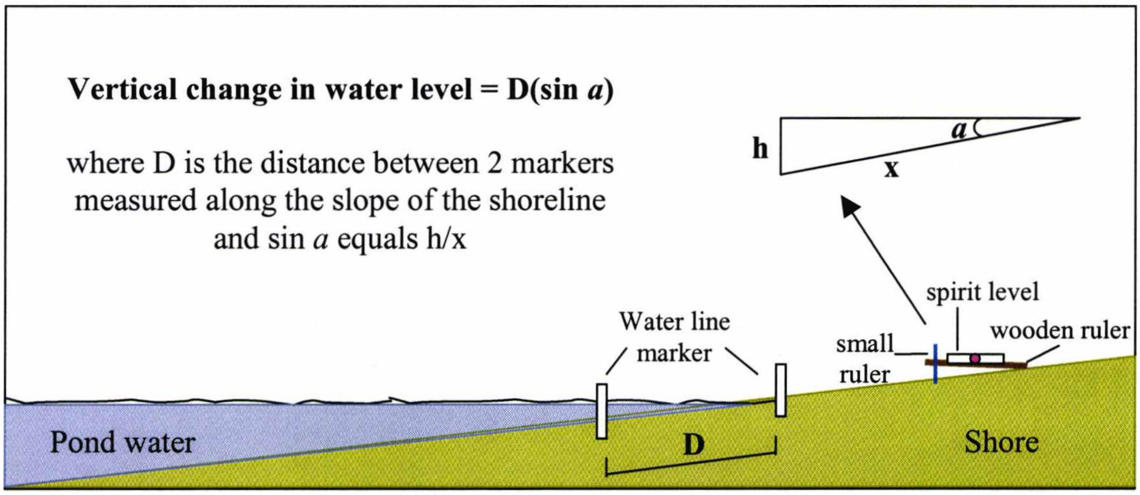


Figure 3.1 Method for measuring changes in pond water level

The range of sin *a* for all ponds was 0.006 to 0.076 (mean = 0.019), demonstrating that this technique was highly sensitive to water movements; a water level drop of only 1 cm, for example, would expose half a meter of shoreline. Wind and resulting small waves introduced a standard error of ± 0.026 cm depth, based on measurements from 10 different days in a non-tidal pond (JOS). The maximum change caused by a moderate wind (approximately 10 m/s) blowing towards the sampling area corresponded with a 0.14 cm rise in water level. To avoid Type I errors (false positives), a conservative 0.2 cm increase in water level was used as the minimum threshold for positive determination of tide-driven water movement in ponds (tidal influence). Water level measurements were conducted on clear days with wind speeds of less than 10 m/s. Measurements after rain showers were excluded from this analysis. Declining water levels were not used to ascertain the presence of tidal influence because ebbing water was not readily distinguishable from evaporative water loss.

To avoid Type II errors (false negatives) in ponds that did not initially show tidal fluctuations, water level measurements were replicated at least 3 times, including during at least one tidal cycle in which the sea rose higher than 25 cm above mean low water (m.l.w). The mean level of high tide during a typical year (1998) was 20 cm above m.l.w (Walker 1992).

The timing and amplitude of sea tides were determined by Walker's 1992 DOS program for worldwide tide predictions, using St. Thomas as the closest reference point. No time correction was used, as the reference point is within 50 km of all ponds except the Anegada ponds, which are within 90 km. Sea level was monitored during February, 1998, using a graduated stake in shallow water at Bluff Bay, Beef Island. The observed timing of high and low tides was approximately equivalent to those predicted by Walker's program. Mean sea levels were calculated as consecutive 5-day means of the difference between m.l.w. and the daily high and low tides.

3.2 (e) Weather

Precipitation data for 1995 through 1998 were supplied by Rowan Roy, who recorded daily rainfall at his house above Hodges Creek (*ca.* 50 m elevation) on Tortola. Data for 1999 through 2001 were supplied by Roger Downing, who reported high and low air temperatures as well as rainfall at his house at Great Mountain, (*ca.* 370 m elevation) on Tortola. No other complete sets of rainfall or temperature data were available for the BVI, and comparisons of precipitation among different locations were not possible.

Ambient air temperature at ponds was measured either with an alcohol-filled laboratory thermometer or with a YSI-85 electronic meter while the probe was inside the instrument casing, which was equilibrated to ambient temperature. These methods reported the same values when used simultaneously. Air temperatures at ponds were determined to be 3°C higher, on average, than temperatures at Great Mountain, and this figure was added to the high and low temperature records reported by R. Downing.

3.2 (f) Evaporation

A drought period between 14 March and 6 May, 1995, during which no rainfall was recorded anywhere in the BVI, offered an opportunity for evaluating long-term evaporation rates in salt ponds. This was accomplished by measuring the change in pond depth at sampling site markers (Section 3.2 (b)) as well as the change in salinity between the beginning and end of the drought period. The resulting evaporation model (see Section 5.2 (a.*ii*)) assumed that the quantity of water lost or gained through the ground was insignificant when compared with evaporative water loss. Nighttime water levels recorded in non-tidal ponds by the method described in Section 3.2 (d) were constant (see Figures 4.3(a), 4.4(a,b) and 4.5(c)), indicating that through-ground drainage was minimal at best. Similarly, depth fluctuations resulting from tidal influence in completely enclosed ponds were negligible when compared with the effect of long-term evaporation.

Evaporation from ponds was expressed as the volume of water lost per day per hectare of pond (see Table 5.2). The volume of water lost was calculated as the change in depth between sampling visits multiplied by the total pond area. This value was divided by the interval between measurement dates, which differed among ponds. The measurement interval was between 27 and 38 days for BAN, BEL and GUA. The interval between depth measurements in SAL spanned 2 months, from 5 March to 14 May, because no depth measurement was made in April, when pond sediments had become too loose to walk out to the site marker. Though this interval exceeded the drought period by 17 days, the quantity of rain that fell during the interval was insubstantial (1.8 cm between 5 and 14 March, and 1.0 cm between 6 and 14 May). Long-term evaporation in JOS and WB could not be calculated because these ponds were completely dry during April, 1995.

A second method for measuring evaporation assessed small changes in water level over a number of hours. These were detected by the method described in Section 3.2 (d) for measuring tidal fluctuations. Only data from ponds in which no tidal influence was detected, BAN and JOS, were used for these calculations of short-term evaporation.

3.2 (g) Groundwater

Groundwater was sampled by digging 4 wells at BLU on 23 January, 1999. These wells were placed approximately equidistantly around the perimeter of BLU. Each well was positioned in areas approximately 30 cm higher than the vegetation line. Another 4 wells were dug at FLA near the access trail at the pond's SSW end on 8 August, 1998. Two of these wells were located at the vegetation line and 2 were located 10 m behind the vegetation line. Wells at BLU were about 1.2 m deep, while those at FLA were about 0.75 m deep. A 5 cm diameter PVC pipe, perforated by slits every 5 cm on alternating sides of the pipe, was placed into each well, and the area around the pipe was refilled with soil. Each well was left for 12 hours to equilibrate. Groundwater was extracted for salinity testing using a long, thin piece of tubing. The level of groundwater was between 10 and 50 cm below the surface. Results are reported in Section 4.2 (b).

3.2 (h) Mangrove mapping

Mangroves were mapped around 14 ponds between July and September, 2000. All mangroves greater than chest-height (*ca.* 1.3 m) were identified and counted within 50 x 10 m belt transects. The length of each transect was measured with a 50 m transect tape, which ran along the pond-side of the mangrove fringe, and the width, projecting into the forest, was estimated. Consecutive transects were placed end-to-end so that the completion of one transect marked the start of the next. All mangroves around the entire perimeter of each pond were thus mapped in 500 m^2 blocks. The representation of each mangrove species was calculated as a percentage of the total number of trees within each transect (see Table 4.3). Mangrove distributions were drawn on existing maps from the BVI GIS database (see Figures 4.7 – 4.16).

The mangrove forest at SAN was assessed first by a visual survey, which determined that only 2 mangrove species were present. A quadrat method was used for quantitative analysis because, unlike other ponds, much of the inundated area was forested. Two 10 x 10 m quadrats were placed at representative forest sites in different areas of the wetland, and all mangroves within each plot were identified and counted. Tree density and proportional representation of mangrove species were calculated from these quadrat data.

The proportional representation of mangrove species at WB was estimated during a perimeter survey in November, 1995, but mangroves at this pond were not mapped.

The potential for predicting major hydrological characteristics of ponds using the proportional representation of mangrove species was evaluated by Discriminant Function Analysis. Four variables, each describing the proportion of one mangrove species across 16 ponds were used to create functions for classifying ponds according to inundation period and, in a separate analysis, according to the degree of sea connection. Ponds were assigned to one of 3 categories in the first analysis: permanent inundation, 6 – 11 months inundation/year, and less than 6 months inundation/year. For the second analysis, ponds were assigned to one of 4 categories reflecting their sea connection: permanent direct connection, periodic direct connection, seawater seep, and no connection. The accuracy of the groupings derived by the resulting functions was evaluated using a cross validation test (see Section 4.2(d.*ii*)).

3.3 Water chemistry analysis

3.3 (a) Salinity

Water salinity was measured *in situ* using a hand-held refractometer with automatic temperature compensation. The refractometer was set to zero in the field before each measurement in order to remove error associated with temperature differences. Instrument resolution was 1 parts per thousand (ppt). Samples having salinities beyond the range of the instrument (100 ppt) were proportionally diluted with distilled water before the final measurement. Instrument error was ± 2 ppt; however, when dilution was necessary, error increased to a maximum of 5% of water salinity. Electronic salinity measurements (using a YSI model 85-50) were found to be inaccurate when compared with refractometer readings. The manufacturer confirmed that a problem with the programmed salinity algorithm led to salinity readings 6% below actual salinity. All reported salinities are consequently refractometer measurements (see Table 5.1 and Appendix B).

3.3 (b) Temperature

Temperature was measured using an alcohol-filled laboratory thermometer with a range from 0° to 100°C with 0.5° divisions. The thermometer was held completely underwater mid-way between the surface and the bottom of a pond for one minute to allow equilibration before a reading was taken. A YSI – 85 hand held electronic meter was used after July, 2000, for temperature readings in water of less than 80 ppt salinity (the maximum range of the instrument). Electronic measurements were compared with simultaneous thermometer measurements, and no discrepancy was found. Temperature readings are reported in Table 5.1 and Appendix B.

3.3 (c) Stratification

Temperature stratification was assessed during dry weather in GUA on 14 July (4 samples between 9:50 and 18:00). Readings were taken with the YSI – 85 near the surface of the pond and also near the bottom of the pond (see Figure 5.5).

Salinity stratification was assessed in BAN on 13 August (16:30 and 20:45) and 14 August (7:00 and 11:50), during dry weather. It was also assessed in GUA after rainfall between 29 July and 1 August, 2000, (6 samples) and between 19 August and 20 August (5 samples). Water was collected from the surface and the bottom in a pipette, and salinity was measured using a salinity refractometer (see Section 5.2 (c)).

3.3 (d) Oxygen

Dissolved oxygen (DO) concentrations (see Table 5.1 and Appendix B) were measured using the Azide Modification of the Winkler Titration (Eaton *et al.* 1995). This method is appropriate for hypersaline water (Sherwood *et al.* 1991), whereas methods using electrode sensors are limited by hypersalinity. Duplicate samples were collected into 60 ml BOD bottles using a non-turbulent sampler; the sampler's water intake was 15 cm above the pond bottom in its deployed position. When ponds were shallower than 15 cm, sample bottles were filled manually by holding them at about the water-column midpoint and controlling water flow and turbulence with the bottle's stopper. Triplicate samples were taken when manual filling was necessary.

DO assays were performed in the field within 10 minutes of sample collection using pre-measured powder-pillow reagents from Hach Company. Results from replicate samples were averaged, but if discrepancies between replicate samples were greater than 1.0 mg/L, sampling was repeated until consistent readings were achieved (discrepancies were infrequent and required no more than one repeated collection). Titrations were performed by the drop method until March 1998, after which a digital titrator (Hach, model 16900-01) was used. Ten assays of the same sample gave a standard deviation of ± 0.2 mg/L with the drop titration method; the digital titration method improved accuracy to a standard deviation of ± 0.05 mg/L.

After July, 2000, dissolved oxygen in ponds with salinities lower than 80 ppt was measured using the YSI-85 electronic meter. Salinities greater than 80 ppt interfered with instrument readings. Results from electronic measurements were compared with titration values for samples collected simultaneously from one location. These methods gave results within 0.2 mg/L of one another when tested on pond water samples in the field.

Diurnal fluctuations in DO (see Figure 5.7) were assessed in BON, FLA, GUA, JOS and RED by monitoring oxygen concentrations over several 24-hour periods between July and September, 2000. Oxygen concentrations were converted to percent saturation in order to normalize data for differences in salinity and temperature. The following formula, derived to predict oxygen solubility in hypersaline waters by Sherwood *et al.* (1991), was used as the denominator in converting dissolved oxygen measurements to percent saturation:

$$\ln C = -6.85693750 \times 10^{4} + 1.28038367 \times 10^{6}({}^{1}/_{T}) + 1.32716777 \times 10^{4} (\ln T) - 4.59371240 \times 10^{1}(T) + 2.65097198 \times 10^{-2}(T^{2}) + S[-4.29122353 \times 10^{-2} + 2.06161380 \times 10^{-4}(T) - 2.68767762 \times 10^{-7}(T^{2})] - 3.60557809 \times 10^{-6}(S^{2})$$

where:

C = equilibrium oxygen concentration at standard pressure of 1 atm, mg/L
S = salinity, ppt
T = degrees Kelvin (Celsius + 273.150)

This algorithm is valid for NaCl-dominated waters up to 260 ppt and between 0° and 35° C (Sherwood *et al.* 1991). Dissolved oxygen measurements from pond waters outside of this range were not converted to percent saturation.

3.3 (e) pH

Measurements of water pH (see Table 5.1 and Appendix B) during 1995 and 1998 were made in the field with ColorpHast Indicator Strips, pH 5 – 10 (EM Science). Resolution using these strips was 0.5. Water samples taken after 1998 were transported to the laboratory, where pH was measured using an electronic meter (pHTestr 2, Oakton). This meter has a specified resolution of 0.1 and is accurate to ± 0.1 (Oakton product information).

3.3 (f) Turbidity

Water turbidity (see Table 5.1 and Appendix B) was measured by the Attenuated Radiation Method (Hach 1997) using a Hach Model DR2010 spectrophotometer at a wavelength of 860 nm. Turbidity was reported in Formazin Attenuation Units (FAU). A standard deviation of ± 2 FAU was obtained in 10 measurements of a stock solution of 50 FAU, while a standard deviation of ± 4 was obtained in 10 measurements using a stock solution of 100 FAU.

3.3 (g) Nutrients

Three forms of dissolved inorganic nitrogen (ammonia, nitrate and nitrite) and one form of dissolved inorganic phosphorous (phosphate) were measured in pond water (Table 5.3 and Appendix C). These forms are routinely used for the evaluation of aquatic ecosystems (Wetzel & Likens 2000).

Water samples were collected in 500-ml plastic collecting bottles. Bottles were pre-cleaned and rinsed with phosphate digestion reagents to remove residual phosphates.

Samples were kept on ice during transportation to the laboratory, where they were either immediately analysed or stored at 4°C. Most samples were analysed within 48 hours of collection. During periods of frequent sampling, as in October, 1998, and July, 2000, longer storage times were necessary, and samples were occasionally frozen for up to 2 weeks before analysis. Turbid samples were filtered before nutrient analysis or before storage when the latter was necessary.

Colorimetric measurements of ammonia, nitrate, nitrite and phosphate concentrations in samples taken during 1995 and 1998 were performed with a Mini 20 spectrophotometer (Milton Roy) using Milton Roy Spectrokit systems. This instrument was replaced by a Hach Model DR/2010 spectrophotometer in 1998. Nutrient tests were similar for both instruments, and they are described below.

Nitrogen as ammonia (NH_3-N) concentrations were measured at 425 nm wavelength by the Nessler Method (Hach 1997). Samples were distilled before analysis because high magnesium concentrations found in concentrated seawater interfere with the colour reaction (Hach 1997). This method detected ammonia concentrations from 0 to 2.50 mg/L NH_3-N, with an estimated detection limit of 0.06 mg/L NH_3-N. A standard deviation of ± 0.02 mg/L was obtained in 10 measurements using a standard solution of 1 mg/L.

Concentrations of nitrogen as nitrate (NO_3^--N) were measured by the Cadmium Reduction Method using pre-packaged reagents (Nitraver V Powder Pillows, Hach). Sample absorbance, measured at 400 nm, detected nitrate concentrations from 0 to 4.5 mg/L. Higher nitrate concentrations were measured at 500 nm wavelength, using the same chemical reaction (Hach 1997).

High chloride concentrations (> 100 mg/L) cause low nitrate readings (Hach 1997). Calibrations using nitrate standards of 1, 2, 4, 6, and 10 mg/L NO_3^--N, each at an NaCl concentration of 40, 70, 100, 150 and 200 ppt, were conducted for the Hach DR/2010 spectrophotometer in 1998 but not for the Milton Roy Mini 20. As a result, nitrate readings of samples prior to 1998 may be inaccurate, particularly in samples with high salinities.

Readings of replicate pond water samples were inconsistent at salinities greater than 40 ppt when using the calibration algorithms developed for the Hach DR/2010. A sample taken at 100 ppt salinity, for example, gave different results when tested at the calibration for a 100 ppt solution than when diluted to 40 ppt and tested at the calibration for 40 ppt and then multiplied by the dilution factor. These inconsistencies may have resulted from changes in the chemical composition of water as various salts precipitated out of solution during evaporative concentration. Ultimately, water samples were diluted to 40 ppt before testing rather than using the higher salinity calibrations. A standard deviation of ± 0.2 mg/L was obtained with the 40 ppt calibration algorithm in 10 measurements using a standard solution of 2 mg/L at 40 ppt NaCl.

Concentrations of nitrite as nitrogen (NO_2^--N) were measured by the Diazotization Method using pre-packaged reagents (NitriVer 3 Powder Pillows, Hach). Sample absorbance, measured at 507 nm wavelength, indicated nitrite concentrations from 0 to 300 μg/L NO_2^--N. The estimated detection limit was 1 μg/L NO_2^--N (Hach 1997). A standard deviation of ± 2 μg/L was achieved using 10 samples of a 100 μg/L NO_2^--N standard solution at 40 ppt NaCl.

Phosphate (PO_4^{3-}) concentrations were measured by the Ascorbic Acid Method (Hach 1997) using pre-packaged reagents (PhosVer 3 Powder Pillows, Hach). Reacted samples were analysed at 890 nm, which detected reactive phosphorous from 0.01 to 5.00 mg/L PO_4^{3-} (Hach 1997). A standard deviation of ± 0.05 mg/L was obtained in 10 measurements using a standard solution of 1 mg/L PO_4^{3-} at 40 ppt NaCl.

Several problems that led to missing data were encountered while testing nutrient concentrations in pond waters. These included overheating of samples during long transport to the laboratory, leaking distillation apparatus (used for NH_3 measurements), and contamination of collecting bottles with soap residues due to multiple users. Where such problems occurred, samples or nutrient readings were discarded.

3.3 (h) Calculation of means

Overall mean values for salinity, temperature, and dissolved oxygen measurements reported for each pond in Table 5.1 were calculated using all values regardless of measurement date, except that measurements taken within 10 days of a previous measurement were excluded (see Appendix B). This was a precaution against biasing the means towards periods of frequent sampling.

Overall mean values for turbidity, pH, ammonia, nitrite and phosphate were based on all samples. Nitrate measurements from 1995 were not comparable with later measurements due to differences in sample treatment and calibration (as described in Section 3.3 (g)). All nitrate measurements are reported (Appendix B), but only readings taken after 1995 were included in mean calculations.

Dates and times for all water chemistry samples are shown in Appendices B and C. It was not logistically feasible to standardize the time of day at which samples were taken, and therefore the reported means are approximate. Means were intended to serve as points of reference for describing the chemical state of BVI salt ponds, but except for salinity means, they do not include the extent of annual or diurnal variation in each chemical parameter. Means of salinity were less affected by the sampling schedule because salinity did not vary diurnally and because roughly equal numbers of samples were taken in all seasons. Salinity measurements prior to 1995 were not included in mean salinity calculations because all were taken during dry seasons.

3.4 Community analysis

3.4 (a) Sampling

Aquatic invertebrates (see Table 6.1) were sampled using a hand-towed plankton net of 80 μm mesh and 12 cm diameter opening at its mouth. Samples taken during 1995 were collected by horizontal tows of this plankton net along a marked transect of 20 m within each pond. Samples taken during other years were collected from a convenient location near the centre of each pond.

Vertical plankton tows, which are frequently used for limnological studies (e.g. Attayde & Bozelli 1998; Jellison *et al.* 2001), were impractical in these very shallow ponds (typically < 0.5 m deep). Horizontal tows effectively sampled the entire water column. The volume of water filtered by a 20 m plankton tow was calculated by multiplying the area of the net by the length of the transect (*sensu* Attayde & Bozelli 1998; Lahr *et al.* 1999), giving a total volume of 230 litres of pond water sampled by each tow. Care was taken to avoid capturing or disturbing sediments with the plankton net, but when this occurred, the sample was discarded and the tow repeated in a nearby undisturbed area. When ponds were very shallow, particularly in the dry season, the plankton net could not be fully submerged. Half-submerged plankton tows sampled approximately 110 litres of water.

Sampling by plankton tow was abandoned in August 1998 in preference for a method that employed a hand pump (made for boat bilges) to bring pond water into a suspended plankton net (*sensu* Dittel & Epifanio 1990) while walking or paddling a surfboard across a relatively deep area in each pond. Fifty full strokes of the pump were taken to constitute a sample, which amounted to 37 ± 0.3 litres of water pumped through the 80 μm plankton net. This pump was replaced in April 2000 by a larger variety, in which 30 strokes constituted a sample of 33.3 ± 0.3 litres. Pumped samples were cleaner than those collected by towing because bottom sediments could be mostly avoided.

Adult-stage aquatic insects (e.g. corixids) were often able to avoid the pump. Each pond was therefore searched visually, especially in shallow areas, for the presence of corixids. Visual searches were also used to determine the presence of other macrofauna, including fish, crabs, *Artemia*, and benthic fly larvae.

The pump method was replaced in 2000 by a light-trapping method. Commercial light traps were too tall for most ponds, so a shallow-design light trap was constructed from a 10 cm diameter by 40 cm length of PVC pipe. Two clear plastic drinking water bottles (caps removed) were cut in half at the middle and pushed mouth-first into each end of the pipe, thus creating entrance funnels which narrowed inside the trap. About 4 cm of the wide-ends of these funnels were slit to make flaps that were folded back over the outside of the PVC pipe, around which rubber bands were wrapped to hold the funnels in place. A small but bright waterproof light rested inside the tube. A 0.9 kg lead weight was tied tightly to the outside of the trap, which then rested on the pond floor. A small float with a ½ m tether acted to mark the trap's location. Light traps were installed after dark and left for at least 30 minutes before collection. This method produced clean samples of planktonic and benthic organisms. It captured several taxa, such as diving beetles, water beetles, nematodes and occasional benthic protists that were never captured by other methods. These additional taxa were not included in analyses comparing pond faunas because of the certainty of false negative records in earlier data.

Benthic plants, algae and microbial communities (see Table 6.1 and Figure 6.1) were characterized *in situ*. Microbial communities and phytoplankton were described in terms of their salient features, such as colour, consistency and layering. During regular monitoring, 6 major categories of photosynthetic communities were recorded: blue-black microbial mat; thin green bacterial mat; red flocculent microbial suspension; red phytoplankton (*Dunaliella*); green phytoplankton; and grass meadows (*Ruppia maritima*).

Fish and large crabs (see Table 6.1) were sampled with a seine and dip net, respectively, for purposes of initial identification only and otherwise were recorded as present or absent by visual inspection. Members of the shore community, including birds (see Table 7.1) and macroinvertebrates (see Table 6.1), were recorded during visual surveys.

3.4 (b) Species identifications

Plants, birds, and large invertebrates were identified using published guides (Acevedo-Rodriguez 1996; Kaplan 1988; Raffaele 1989). Difficult plant identifications were verified by Pedro Acevedo-Rodriguez of the United States National Museum of Natural History (USNMNH) Smithsonian Institution.

Cyanobacteria and diatoms were identified by David Garbary (St. Francis Xavier University, Nova Scotia). Algae were identified using Taylor (1960), and identifications were confirmed by Lisa Muehlstein (Jacksonville University).

Molluscs were identified by Fred Kraus (Bishop Museum) and deposited at the University of Florida's Natural History Museum.

Tiger beetles were identified by Michael Ivie (Montana State University). Additional tiger beetle specimens were deposited at the USNMNH. Shore bugs (hemipterans) and aquatic beetles were identified by Dan Polhemus, Paul Spengler and Warren Steiner (USNMNH) and deposited at the USNMNH. Water boatmen (corixids) were identified using Hungerford (1948) and specimens were deposited at Cornell University and at the USNMNH. Midge larvae were identified by John Epler in Florida. Brine fly larvae (*Ephydra*) were identified using Courtney *et al.* (1996) and Pennak (1978) and confirmed by Wayne Mathis of the USNMNH. Mosquito larvae were identified using Walker & Newson (1996).

Brine shrimp (*Artemia*) were identified using Dodson & Frey (1991) and confirmed by Denton Belk (Our Lady of the Lake University, San Antonio). *Artemia* specimens were deposited at the LACMNH. Rosalie Maddocks (University of Houston) identified the ostracods. Janet Reid (USNMNH) initially identified copepod specimens. Under her guidance, copepods in 14 plankton samples, collected from several ponds at various salinities, were dissected and identified to species. Copepods were deposited at the

USNMNH. Fiddler crabs and their larvae were identified by Todd Zimmerman (Los Angeles County Museum of Natural History, LACMNH) and deposited at the LACMNH.

Fish were identified using Böhlke & Chaplin 1993; identifications were confirmed by Graham Forrester (University of Rhode Island).

Generic names and common names rather than specific names are used for ease of reference in this thesis.

3.4 (c) Density estimations

Quadrat sampling was used during 1995 to determine the abundance of adult fiddler crabs inhabiting pond shores. A 0.25 m^2 quadrat was thrown arbitrarily so that it landed on the pond shore just below the vegetation line, and all fiddler crab holes fully or mostly within the quadrat were counted. Results from 6 replicate quadrat counts were used to calculate the density of crab holes per square metre of unvegetated shore at each pond. Hole densities gave relative estimates of crab abundance, obviating the need for invasive sampling methods.

Zooplankton was counted under a 10 – 50X Zeiss stereoscope. Each organism in every sample was identified to the lowest possible taxonomic level at low magnification without dissection. Species within the subclass Ostracoda or within the copepod genus *Cletocamptus* were not distinguished in density counts. Juvenile and adult stages of *Artemia* were combined, but nauplii were not counted. Members of the protist phylum Ciliophora and the animal phylum Rotifera were noted as present but not counted. Samples that could not be analysed within 8 hours of collection were preserved in alcohol, but this practice was avoided whenever possible because the presence of certain taxa, particularly rotifers and ciliates, was difficult to determine after preservation.

Each plankton sample was concentrated using an 80 μm sieve, and the retained sample was placed in a petri dish with pond water from the same sample. A grid placed under the petri dish aided counting. All individuals of larger taxa, such as *Artemia* and *Trichocorixa* (water boatman), were counted unless the total number in the sample was greater than 300, while all individuals of smaller taxa, such as the copepods, were counted unless the total number was greater than 100. Samples with greater numbers of individuals (i.e.>100 or >300) were subsampled and then counted. When subsampling was necessary, each sample was standardized to a volume of 100 ml, from which three 5 ml subsamples were taken, and all individuals within these subsamples were counted.

The precision of plankton counts was tested by analysing samples from 6 replicate plankton tows and comparing the ratio of the standard deviation (SD) of counts to count means for several taxa. Replicate tows were distributed across each pond so that each sample was taken approximately 30 m away from other samples. In 6 replicate tows from BAN on 17 September, 1995, *Artemia* was the only planktonic representative in all samples (mean count 0.08 ± 0.05 ind./L), and the standard deviation of replicate samples was 63% of mean number of *Artemia*. This test was repeated in JOS on 5 November, 1995, when the standard deviation of replicate tows for *Trichocorixa* (mean count 0.50 ± 0.23 ind./L) was 46% of the mean, for cyclopoid copepods (mean count 6.7 ± 5.4 ind./L) the SD was 81% of the mean, and for copepod larvae, which were subsampled, (mean count 650 ± 380 ind./L) the SD was 58% of the mean. The same test was conducted for plankton-pump samples taken from BAN on October 10th, 1998, when *Artemia* was again the only planktonic animal present (mean count was 0.05 ± 0.03 ind./L). The standard deviation of replicate samples was 60% of the mean count. No variation in the number or representation (presence/absence) of taxa was found in any of these sets of replicate samples. It is expected, however, that false negative results were likely when very small organisms, such as rotifers, ciliates, and possibly copepods, were present at low densities.

The plankton density data were highly skewed because individual taxa were more often absent (zero abundance) than present in the data set. Normalization by log transformation was not possible as the log of zero is undefined. Because of the skewed data distribution and the substantial error inherent in plankton sampling methods, all plankton data were converted to presence/absence scores before being used in statistical analyses.

During a study of hurricane impacts in 1998, qualitative scores were used to describe plankton abundance in BLU, LON and JOS. Each taxon in a plankton sample was given an abundance score between 0 and 3, with 0 indicating absence and 3 indicating high density. These scores were relative to the mean densities of each taxon being assessed. That is, a score of 3 for *Trichocorixa* represented fewer individuals per litre than a score of 3 for rotifers, since rotifers, when observed, were normally in higher abundance than *Trichocorixa*.

3.4 (d) Sampling schedule and data matrices

A total of 235 biological sampling visits was made to 17 ponds between 1991 and 2000. Collected data were assigned to 3 data matrices (Table 3.1 and Appendix A). The first (1995) represents 110 site visits during which samples were taken monthly from 10 ponds in 1995.

Table 3.1 Number of samples in 3 data matrices

	Data Matrix:			
Pond	1995	Other years	Hurricane	Total # samples
BAN	12	12	19	43
B.I. Salt Flats	0	1	0	1
BEL	12	12	0	24
BLU	0	2	0	2
BON	10	7	0	17
FLA	10	7	0	17
Great Thatch	0	1	0	1
GUA	11	18	6	35
JOS	12	7	8	27
LON	0	4	7	11
Manhead	0	2	0	2
PTP	10	3	0	13
RED	10	4	0	14
RUN	0	2	0	2
SAL	11	0	0	11
SIN	0	2	0	2
WB	12	1	0	13
Total	110	85	40	235

Logistical difficulties occasionally prevented sampling, particularly in some of the most inaccessible ponds. The remote Anegada ponds, for example, were visited in all months except June and December. On 12 of the 1995 site visits to various ponds, water level was either too low to permit a plankton tow or the pond was completely dry. Two samples partially spilled during transport. Taxa present in the remaining sample were identified, but density estimates were not attempted. These and other circumstances are indicated for each sample in Appendix A. Density values derived from the remaining 96 samples were used to compare seasonal changes in zooplankton composition among ponds (see Figure 6.6).

The second data matrix (other years) represents 85 samples taken from 1991 through 2000. These data were combined with the 1995 data and reduced to binary presence/absence scores in order to analyse the distribution of each taxon across a natural mosaic of salinity conditions, as described in the next section.

The third data matrix (hurricane) represents 40 samples from 4 ponds that were taken before and after hurricanes in 1995 and 1998. These data were used to track changes in community structure after hurricanes (see Figures 6.10 and 6.11).

3.4 (e) Logistic regression analysis

Aquatic communities that inhabit chemically distinct habitats have been compared using cluster analysis (e.g. Amaral & Costa 1999; King *et al.* 1996), principal components analysis (e.g. Armengol & Miracle 1999; Blinn 1993; Sprules 1977) or both (Green & Vascotto 1978). Few studies have assessed biotic responses to water chemistry that varies temporally within hypersaline habitats, but these have used canonical correspondence analysis (Attayde & Bozelli 1998; Carruthers *et al.* 1999), ANOVA (e.g. Dittel & Epifanio 1990) or various forms of regression analysis (e.g. Lahr *et al.* 1999; Therriault & Kolasa 1999). This study took on the particular challenge of evaluating the responses of an aquatic community to spatial changes (among ponds) and temporal changes (within and among ponds) in chemical conditions. Salinity was used as an indicator of pond chemistry, as described in section 3.1.

Logistic regression analysis was chosen to describe the specific relationships between individual taxa and salinity. Logistic regression is a special case of the generalized linear model. It fits probabilities for the response levels using a logistic function, and it makes no assumptions about the distribution of independent variables (ter Braak & Looman 1987). This test was particularly appropriate because the plankton data were entered as binary values (presence/absence see Section 3.4 (c)), and such values do not follow normal distributions. It was necessary to pool samples from different ponds and different dates because logistic regression uses a chi-square test that is only valid for large data sets (ter Braak & Looman 1987). It was assumed that any common taxon could occur in any pond in which it occurred at least once and in which environmental conditions were appropriate for its survival. Therefore, all samples were treated as independent, but if a taxon was never recorded from a pond, then all data from that pond were excluded in the regression analysis for that taxon. Presence/absence scores for each taxon were regressed against all salinities between 35 and 350 ppt.

Some data points were excluded in order to avoid confounding the analysis with what were judged to be abnormal samples or extreme conditions. Pond water below 35 ppt. was not hypersaline, occurred infrequently and in 2 ponds only, and was therefore considered abnormal (7 samples excluded). Pond water above 350 ppt exceeded the physiological limits to life and was considered extreme (3 samples excluded).

Heavy rainfall abruptly reduced pond salinities. Carruthers *et al.* (1999) showed that biotic responses to physical and chemical changes in an estuarine environment range from immediate to a lag time of 6 months. In the present work, a lag time of 2 weeks after heavy rainfall, representing a minimum best-guess lag interval, was used to exclude samples considered unrepresentative of equilibrium communities (17 samples excluded). Additionally and in order to avoid bias, samples from the same pond were separated by an interval of at least 10 days in the logistic regression data matrix (10 samples excluded). A total of 158 samples were included in the logistic regression analysis; 84 of these samples were taken in 1995 and 74 were from other years.

Logistic regression in the JMP Version 3.2 statistics package (SAS 1997) was used to model the relationship between salinity and the probability of occurrence for each taxon (see Figure 6.7). The probabilities predicted by the model were used to determine the range of salinities at which each taxon is likely to occur (see Figure 6.8). Probability levels of 0.3 or higher were chosen as a reasonable designation for likely occurrence because the highest probability of occurrence for most taxa was lower than 0.8.

The fit of each regression model was evaluated using the difference in negative log likelihood from the model fitted by the data and a model that omits all the regressor effects except the intercept parameters (known as the whole model test, SAS 1995; see Table 6.5 for results). This is a chi-squared test of the hypothesis that all regression parameters are zero (which would give a flat regression line). A value of $p \leq 0.050$ was considered a significantly good fit. In addition, a lack of fit test (also called goodness of fit) was performed (see Table 6.5). This is a chi-squared test used to evaluate whether enough information exists in the included variables or whether more terms are required to model the data (SAS 1995). A value of $p \leq 0.050$ was considered a significantly poor fit. If either test (insignificant whole model test or significant lack of fit) indicated a poor fit, the square of salinity was added as a second regressor in the model, effecting a quadratic regression analysis (see Figure 6.7). The Wald statistic was used to determine whether salinity alone or combined with the square of salinity showed a significant effect on the occurrence of a taxon (see Table 6.5). The Wald chi-squared is an approximation of the whole model test. While it is considered less trustworthy, it allowed the comparison of each effect in the quadratic models (SAS 1995).

3.4 (f) Analysis of species associations

The potential for biotic interactions existed for species that overlapped both in their salinity range and in their distribution among ponds. Multiple 2-sided Pearson Chi-Square tests (SPSS 1999) were performed to identify associations between pairs of taxa. The logistic regression data matrix (described in Section 3.4 (e)) was edited for each test to include only those ponds in which both members of a pair of taxa occurred and to remove points at which one or both species had 0.3 or less probability of occurrence (as predicted by logistic regression, Section 3.4 (e)). For each pair of taxa, the edited data set was used to create a 2 x 4 matrix indicating the number of occurrences in which a) both species were absent, b) both were present, c) the first was present without the second d) the second was present without the first. The Chi-Square test was applied to this matrix (see Table 6.6).

In addition, a Student's t-test was applied to 11 samples in which *Cletocamptus* had been identified to species in order to determine whether *C. dietersi* and *C. albuquerquensis* occupied different ranges of salinity (see Figure 6.9). This determination could not be achieved with the logistic regression data matrix as described in Section 3.4 (e) because these species were not distinguished in other samples.

3.4 (g) Bird populations

Bird counts (N = 107) were performed monthly at 10 ponds during 1995 (see 1995 data matrix, Appendix A, for dates and times), but the occurrences of bird species, particularly new records, were noted during all pond visits. Time of sampling was not standardized, but sampling effort was standardized to 30 minutes, and all bird counts began immediately upon approaching each pond. Birds were viewed with 10 x 50 binoculars. Any bird seen too briefly for positive identification was not counted. Birds that inhabited the peripheral vegetation were not counted unless they were at the edge of a salt pond at the time of sampling.

The overall frequency of occurrence in bird counts is reported for each species (see Table 7.1). Mean abundance (see Figure 7.2) is reported only for commonly occurring species because the likelihood of error associated with these summary statistics is greater for uncommon species. Overall species richness (the total number of species recorded), momentary species richness (the mean number of species encountered on each visit) and bird abundance were compared among ponds (see Table 7.2).

A survey of feeding behaviours intended to identify prey items was conducted for 7 common species, which were individually observed for 30 minutes following bird counts in March and April of 1995 (see Section 7.2 (d)).

Scatter plots were used to compare the abundances of each of the 4 most common species with prey density (see Figure 7.3). Prey density was represented as the number of macroinvertebrates per litre, including *Ephydra, Dasyhelea, Artemia* and *Trichocorixa* (data presented in Section 6.2 (d.*i*)). All bird counts, irrespective of location, were pooled for this analysis, and one data set was created for each of the 4 species evaluated. These data sets were normalized as follows. Bird counts made between April and September, when most species were least abundant, were excluded in order to reduce variation due to seasonal differences in abundance. Counts from each pond at which a particular bird was not abundant (less than a mean of 5 individuals per count) were excluded in order to limit each data set to ponds in which a bird was most likely to occur.

A positive relationship between a bird's abundance and prey density was expected to show a triangular rather than a linear distribution of points in a scatter plot because birds may be absent from ponds for reasons other than food availability (e.g. weather, time of day, etc.).

This chapter provided a comprehensive description of the approach taken and methods used in this study. The following chapter is the first of the data chapters, and it describes hydrological aspects of salt ponds in the BVI.

Chapter 4: Hydrology

4.1 Introduction

Wetlands are dynamic ecological systems that evolve through a series of natural change. Many of them are only temporary features of the landscape as this procession of natural change leads to the disappearance of some wetlands and the creation of others elsewhere (Barbier *et al.* 1997). Succession via land building and changing hydrological conditions has recently been described by McKee & Faulkner (2000) for a mangrove-lined saline pond on Cat Cay, Belize. Similar processes should occur in the salt ponds of the BVI, and, consequently, present-day ponds should represent stages in a natural hydrological progression, from near-marine systems to near-terrestrial systems. This study, the first to include a large number of ponds, provides a unique opportunity to assess hydrological change by examining variation among salt ponds. Understanding the relationships between hydrological processes and biotic responses is essential in wetland restoration efforts (e.g. Haltimer *et al.* 1997), which are currently being considered in the BVI (Bert Lettsome, pers. comm. 2002)

Factors that influence the hydrology of wetlands include precipitation, catchment size, groundwater flow, surface flow, permeability of sediments, and vegetation. Precipitation in the BVI is seasonal, and salt ponds occur at the bottom of steep watersheds on all islands except Anegada, which is flat. Rainwater tends to run down hillsides over the surface rather than through the ground because the soil layer is thin and the underlying rock has low permeability (MacDonald *et al.* 1997). Surface flow occurs only after heavy rainfall, as there are no permanent rivers, creeks or streams in the BVI. Groundwater resources, which are limited to narrow alluvial valleys, scattered sand deposits and fractured volcanic rock, recharge at a rate of only 3 to 8 cm/yr (MacDonald *et al.* 1997). Seawater, on the other hand, may enter salt ponds over the surface or through the ground because the berms that separate salt ponds from the sea are composed of permeable sediments, mainly sand and coral rubble (Rooth 1965). Seawater input is predicted to be an important force in controlling pond hydrologies.

Vegetation is generally considered to be an important indicator of wetland hydrology. The standard for identifying a wetland in the United States, for example, has been defined as "those areas that are inundated or saturated by surface or groundwater at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions" (Environmental Laboratory 1987, App. A). The internationally accepted Cowardin system for wetland classification specifically uses vegetation characteristics for distinguishing among wetlands that share a similar hydrology, geomorphology and chemistry (Cowardin *et al.* 1979).

Hydrophytic vegetation at BVI salt ponds is represented most conspicuously by 4 species of mangrove trees, red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*) and buttonwood (*Conocarpus erectus*). Studies of mangrove zonation have shown that these species are highly specialized to particular edaphic conditions which are determined by local hydrology (Bacon 1994; Blasco *et al.* 1996; Imbert *et al.* 2000; Kathiresan & Bingham 2001; Lewis 1990; Lugo & Snedaker 1974; McKee & Faulkner 2000; Wolanski 1992). Lugo & Snedaker (1974) showed that red mangrove was most productive when developing in low salinity soils, while under high-salinity conditions black mangrove was more productive than red mangrove and white mangrove was more productive than black mangrove. Ellison & Farnsworth (1993) showed that red mangrove was more tolerant of inundated soils (at low salinity) than was black mangrove. Furthermore, McKee (1995) showed that Caribbean mangroves responded differently to increased soil nutrients. White and black mangroves grew faster than red mangrove when nutrients were high, while low nutrients minimized interspecific differences in growth rate.

Tidal fluctuations form gradients of salinity, water saturation, and redox potential (an index of soil aeration) in wetland soils, and these gradients are strongly correlated with mangrove distributions (Imbert *et al.* 2000). As a result of these sharp gradients, the mangrove community is normally zoned, with red mangrove occurring closest to the seashore, black mangrove occurring in more elevated soils with higher pore water salinity, white mangrove occurring on the landward side of mangrove zones in brackish, waterlogged soils and buttonwood restricted to shallow or well drained soils of intermediate salinity (Imbert *et al.* 2000). Blasco *et al.* (1996) has suggested that mangroves may be useful in interpreting hydrological variation in tropical wetlands because of this strong relationship between species distribution and hydrological conditions, which are in large part determine by tidal regimes.

This chapter assesses hydrological variation among salt ponds by comparing the relative influences of seawater and rainwater among ponds. Mangrove distributions are compared with other hydrological characteristics to determine their value as indicators of hydrological variation among salt ponds.

4.2 Results and discussion

4.2 (a) Inundation and seasonal depth fluctuations

Differences in the duration of inundation and in the degree of connectedness with the sea were apparent among ponds (Table 4.1). While some ponds never dried (permanent ponds), others were inundated for only a few months each year (non-permanent ponds). Many ponds received inputs from both rainfall and from seawater inflow, but the degree of seawater influence varied among ponds. Ponds that were permanently connected with the sea were also permanently inundated (BON, FLA, PTP & RED). Two permanently inundated ponds (BEL & SAL) received small seawater inputs via through-ground seeps rather than via aboveground connections. Some non-permanent ponds were periodically connected with the sea (LON & WB), while most ponds, both permanent and non-permanent, had no visible sea connection. Evaporation was an important force in all ponds, as illustrated by a depth reduction (and salinity increase, as described in Section 5.2 (a.*ii*)) in all ponds monitored during the 1995 dry season (February – May, Figure 4.1). The following sections describe groups of ponds that share major hydrological characteristics, which are shown in Table 4.1.

4.2 (a.*i*) Non-permanent ponds with no visible sea connection

HAN, LEE, NOR and SAN held water only for short periods after rainfall, and they were inundated for a total of 3 to 4 months annually. BLU, RUN and JOS were also greatly influenced by precipitation, but these ponds maintained inundation for 7 months or more in most years.

The influence of rainfall on water depth in 1995 is shown for JOS in Figure 4.1(a,b). JOS was either completely dry or was covered with a very shallow layer of water (1.5 to 8 cm) from February through August. A rainstorm on May 7th and 8th, 1995, precipitated 1 cm of rain, inundating JOS to a depth of 8 cm. Further rains in May maintained inundation in JOS, but dry weather and evaporative conditions in June led to desiccation by July. JOS remained dry through the first half of August despite episodic rain showers. Hurricane rains in September filled JOS to a depth of 29 cm, and subsequent rains maintained and increased this level over the next few months.

The intensity of rainfall may play a role in pond inundation, as more water should run off hillsides and into ponds during periods of intense rainfall than during periods of lighter rain, which is more likely to be absorbed by soil and vegetation. JOS, for example, was inundated by 1 cm of rain in early May but it remained dry throughout rains of similar or greater quantity in late July. It was not possible to assess the effects of rain shower intensities because intensity of rainfall during 1995 was not measured and because the frequency of depth measurements was insufficient for such analysis.

Table 4.1 Hydrological characteristics of ponds

Pond	**Area (ha)**	**Perim. (m)**	**Dist. to sea (m)**	**Water-shed (ha)**	**Surface connection with sea**	**Sediments**	**Inun-dation (mo/yr)**
BAN	3.0	1,035	37	11	none	organic mud	12
BEL	13	1,700	44	41	seep	organic mud	12
BLU	3.6	920	60	40	none	sand/mud	8
BON	57	5,000	170	85	direct	organic mud	12
FLA	220	9,900	160	330	direct	calcite/gypsum	12
GUA	1.9	610	180	18	none	sand	12[a]
HAN	0.40	270	10	20	none	sand	3
JOS	9.0	1,500	110	150	none	sand	7
LEE	0.32	270	20	11	none	sand	3
LON	8.6	1,300	20	18	periodic	sand/mud	9
NOR	0.42	280	80		none	sand	4
PTP	72	5,600	150	110	direct	sand	12
RED	110	6,300	300	170	direct	calcite/gypsum	12
RUN	4.7	1,000	40	13	none	sand/mud	7
SAL	4.0	890	46	13	seep	organic mud	12
SIN	1.5	640	12	10	none[b]	organic mud	12
WB	1.8	2,400	42	27	periodic	organic mud	10

[a] inundation in GUA was artificially maintained (see Section 4.2 (a.*i*)

[b] possible underground connection (see Section 4.2 (d.*iv*))

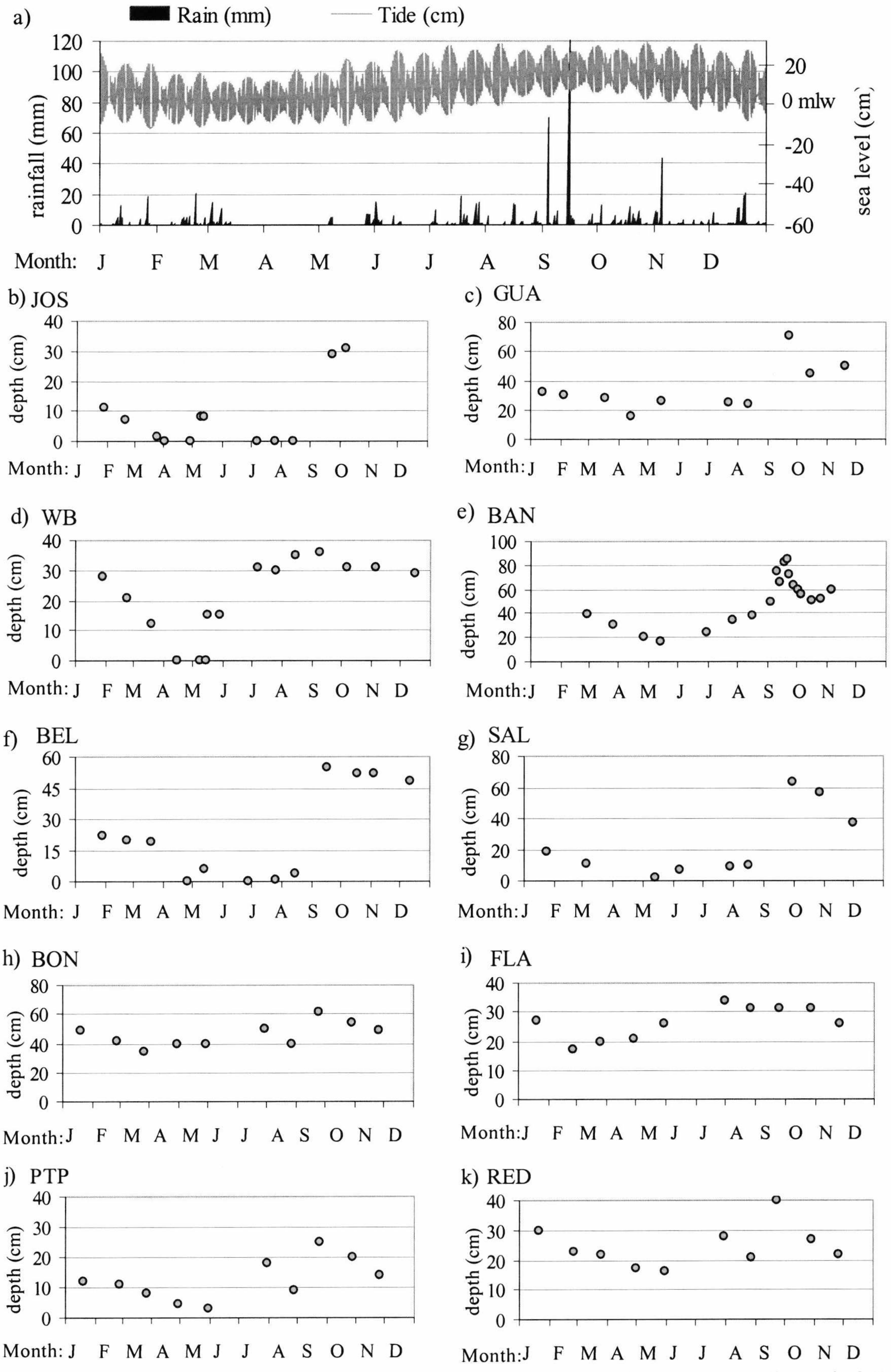


Figure 4.1 Annual depth fluctuations in ponds during 1995 with corresponding rainfall and tidal cycles

GUA was a temporary (non-permanent) pond until 1990, after which saline water input via an overflow pipe and an effluent pipe from a nearby desalination plant resulted in permanent inundation. Regular input of seawater maintained a relatively stable water level in GUA for most of the year (Figure 4.1(c)). Pond depth at GUA was, nevertheless, affected by weather patterns, as is illustrated by a 12 cm drop in water level during a drought in April,1995, and by a 47 cm rise in water level after the hurricane rains of September, 1995 (Figure 4.1(c)).

4.2 (a.*ii*) Non-permanent ponds with periodic direct sea connection

A low point in the berm at WB was breached by high seawater each summer and seawater connection through this channel was maintained by seasonally high sea level through December. Inundation by seasonally high tides is illustrated in Figure 4.1(a,d). WB had evaporated to dryness during a long period of drought in April and May, 1995. The low-volume rains of May 8th and 9th, which inundated JOS, did not fill WB, presumably because of its smaller watershed area (Table 4.1). A high tide of 23 cm above mean low water (m.l.w.; Figure 4.1(a)) which was the first tide of this magnitude for the year, occurred in conjunction with a full moon and filled WB to a depth of 15 cm with seawater overnight (Figure 4.1(d)). Water level in WB did not fluctuate greatly as long as the connection with the sea was maintained. The hurricane rains of September had no effect on water level in WB. Direct connection with the sea during the hurricanes presumably allowed rapid equilibration of water level in WB by draining runoff to the sea.

Episodes of seawater inundation, similar to those in WB, were observed over several years (1998 to 2001) in LON, although depth was not monitored in this pond. Three concrete culverts, constructed to allow water to drain under the road that separated LON from the shore on the southern side of the pond, allowed seawater into LON in summer and fall when sea level was highest.

Each year, high tides early in summer inundated LON and carried fish, crabs and shrimp into the pond from the seashore mangrove community. These marine animals were stranded in the pond by a receding tide. Hypersalinity and high temperatures, caused by evaporation and insolation, killed the stranded marine animals. Frigate birds and herons gathered to feed on the stranded and dying fish. These stranding events did not occur during later months when the mean sea level was high enough to maintain a more constant water exchange in LON.

During periods of lower sea level (mid-January to mid-May), water levels in LON and WB were determined by weather. WB showed a gradual decline in water level beginning in January, when the mean sea level dropped below 6 cm above m.l.w. and the maximum high tide remained lower than 17 cm above m.l.w. (Figure 4.1(a,d)). The timing of lower sea level corresponded with the onset of the dry season, and both WB and LON evaporated to dryness by April of each year between 1995 and 2002.

4.2 (a.*iii*) Permanent ponds with no visible sea connection

BAN and SIN were both permanently inundated despite having no visible sea connection. BAN lost 22 cm in depth during a dry period between late February and early May, 1995 (Figure 4.1(e)). During this time the inundated portion of BAN shrank to approximately 60% of its prior area, and much of the pond bottom was exposed. The water level rose gradually between June and mid-August. It is not clear whether this was due to increased frequency of rain showers or to increased tidal height, but the lack of tidal fluctuations in BAN (see Section 4.2 (c)) points to increased rainfall as the responsible agent. However, evidence from JOS, which remained dry during the same period (June and mid-August), indicated that rainfall did not keep up with the rate of evaporation during this period.

Higher sampling frequency during September and October showed the effect of rainfall on water level in BAN more precisely (Figure 4.1(e)). Hurricane Luis, on September 4th, precipitated nearly 7 cm of rain and raised the level of BAN by 26 cm to a depth of 75 cm. Shortly after this, the water level in BAN fell by 9 cm, presumably via drainage through the sand and coral berm that separated BAN from the sea. Hurricane Marilyn precipitated 13 cm of rain between September 15thand 18th, and this, along with a further 1.3 cm of rainfall over the following few days, raised BAN water level 19 cm to a depth of 85 cm. Water level again dropped shortly after the hurricane, this time by 13 cm, and it continued to fall through mid-October despite continued rain showers. Through-ground drainage of pond water to the sea, which resulted in a rapid drop in BAN's water level after each hurricane, was only evident when water level was exceptionally high, and it did not appear to be an important source of water loss at other times.

As in non-permanent ponds without sea connection, water level in BAN was controlled by rainfall and evaporation. BAN was approximately twice as deep as non-permanent ponds, and it consequently had a lower proportion of surface area exposed to evaporative forces. Deeper water may prevent BAN from evaporating to dryness.

Unlike BAN, SIN exhibited a relatively constant area of inundation throughout the dry season, although depth was not specifically monitored in this pond. This suggests that SIN was not greatly influenced by rainfall and evaporation cycles.

4.2 (a.*iv*) Permanent ponds with seawater seeps

BEL and SAL were both permanently inundated and received small but constant seawater input through a single seep at each pond. Salinity of water emerging from these seeps was consistently near 40 ppt, which indicated a seawater origin. The seeps were located above the level of the water in each pond. The berm in the seep area at SAL was composed of coral rubble, while the berm in the seep area at BEL was composed of organic and silty sediments. Depth fluctuations in these ponds were similar to one another (Figure 4.1 (f,g)), and both ponds responded to rainfall and evaporation cycles. BEL and SAL became shallow and shrank in area during the drought period in March and April, 1995. The water level at BEL declined below the marked sampling area and exposed the depth reference point, hence the zero depth values for April, June, and July. With increasing sea level between June and August, 1995, (Figure 4.1 (a)) greater seawater input through seeps at BEL and SAL was expected. Contrary to expectation water level in these ponds did not rise in the summer. Rains from the September hurricanes, however, raised the water level more than 50 cm in both ponds. These results indicate that depth in permanent ponds with seawater seeps is mainly controlled by rainfall and evaporation, though seawater seepage may prevent desiccation during dry periods.

4.2 (a.*v*) Permanent ponds with direct sea connection

The Anegada ponds, BON, FLA, PTP and RED, maintained a direct connection with the sea through a narrow channel near PTP (see Figure 2.3). This channel measured 3.3 m wide and 37 cm deep at its narrowest point. A current flow of 12 cm/sec was measured in this channel as water from the ponds drained out after a low tide on 22 April, 2000. Depth fluctuations in these ponds were generally similar to one another, and the ponds responded to seasonal changes in mean sea level more so than to rainfall and evaporation cycles (Figure 4.1 (h-k)). Both rainfall and elevated sea levels associated with windstorms (storm surges) should contribute to elevated pond water levels during hurricanes, such as those in September, 1995, but water levels in ponds with direct sea connection should equilibrate rapidly after such storms. However, in BON, PTP and RED water levels were still elevated 9 days after the September hurricanes passed (Figure 4.1(h-k)). It is possible that groundwater trapped in Anegada's limestone substrate continued to feed into these ponds after the hurricanes, thus maintaining the elevated water levels observed. Over the following month, water levels in these ponds fell to pre-hurricane levels.

4.2 (b) Groundwater

Salinity in groundwater wells at the vegetation/shore border of FLA averaged 81 ± 4 ppt on 9 August, 1998, while the pond salinity was 89 ppt. No halocline was detected in the groundwater wells. Ten meters behind the shore vegetation where the mangrove fringe began, groundwater salinity (46 ± 0.7 ppt) was closer to that of seawater. This sharp change in groundwater salt concentration is typical of the interface between salt flats and mangroves (Kathiresan & Bingham 2001).

At BLU, groundwater salinity averaged 54 ± 6 ppt on January 23, 1999, while the pond salinity was 41 ppt. Groundwater salinity showed only a small increase to 62 ± 10 over the following 2 months, during which time the pond lost 27 cm in depth and gained 64 ppt in salinity via evaporation (Figure 4.2).

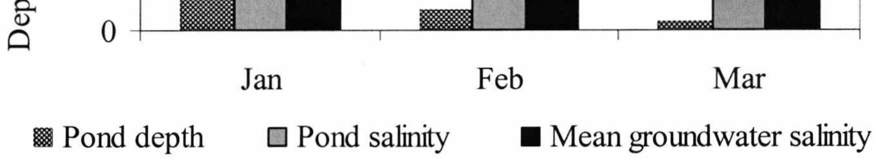


Figure 4.2 Groundwater salinity at BLU, January – March, 1999

The constant hypersalinity of groundwater near ponds, particularly during the latter part of the rainy season (January), suggests that seawater was a more important source of groundwater than rainwater was. Freshwater inputs to ponds, therefore, are likely to be brief events of surface runoff during rainfall.

4.2 (c) Tide-induced water level fluctuations (tidal influence)

Table 4.2 and Figures 4.3 – 4.6 show daily water level changes in several ponds. No tidal influence on water level was found in BAN, GUA and JOS (Figures 4.3(a), 4.4(a,b) and 4.5(c), respectively) . HAN, LEE and NOR were presumed to be non-tidal because the bottoms of these ponds appeared to be above sea level, and they remained dry for most of each year.

Water level in BLU, LON and RUN (Figures 4.3(b – d)) was tidally influenced, but this influence was not always detectable. Tide-induced fluctuations were detected on 2 out of 4 measurement periods in BLU (Table 4.2). An uncharacteristically large water-level change (1.7 cm rise) occurred in BLU on 30-31 January, 2001 (Figure 4.3(b)). This change did not correspond with high sea level, nor could it be explained by other prevailing factors such as rainfall or wind. Rather, the full range of water level change in BLU may have been missed on other sampling dates when the duration of sampling was shorter (12 hours) than that of the January measurement (18 hours). This problem was not apparent in LON or RUN (Figures 4.3(b – d)) because high water levels in these ponds occurred shortly after the high tide, while in BLU the pond-level high was greatly delayed (e.g. by approximately 10 hours on 30 January, 2001, Figure 4.3(b)). RUN showed consistent responses (0.3 to 0.4 cm) to tides except on 27 October, 2001, when the measured rise (0.04 cm) in water level was below the threshold for detection. LON generally showed higher-magnitude changes in water level than other Beef Island ponds, but during times of lower sea level, as on 30 to 31 January, 2001, it lost direct connection with the sea (see Section 4.2 (a.*ii*)) and tidal fluctuations were not detected (Table 4.2, Figures 4.3(b – d)).

WB showed a small increase (0.19 cm) in water level (Figure 4.4(c)), but it was sampled only once (in April, 2000) during the period of low sea level. Tidal water level fluctuations are undoubtedly experienced in WB at other times of the year when it is connected with the sea.

The water level in BEL rose substantially (0.7 cm) in response to a rising tide on 10 July, 2000, the only date on which it was sampled (Figure 4.5(a)). A water-level rise of 2.6 cm at SIN (Figure 4.5(b)) was higher than that measured in any other pond and occurred in response to a moderate high tide of only 14 cm above m.l.w. All of the Anegada ponds showed regular water level fluctuations in response to tidal cycles, and water levels in all ponds closely followed that of tides (Figure 4.6).

A specific determination of the amplitude and delay of water level responses to tides was not conducted in this study. Such a determination requires more frequent measurements, and this is recommended as a goal for future research as it should provide a more detailed understanding of the variability of tidal influences among ponds.

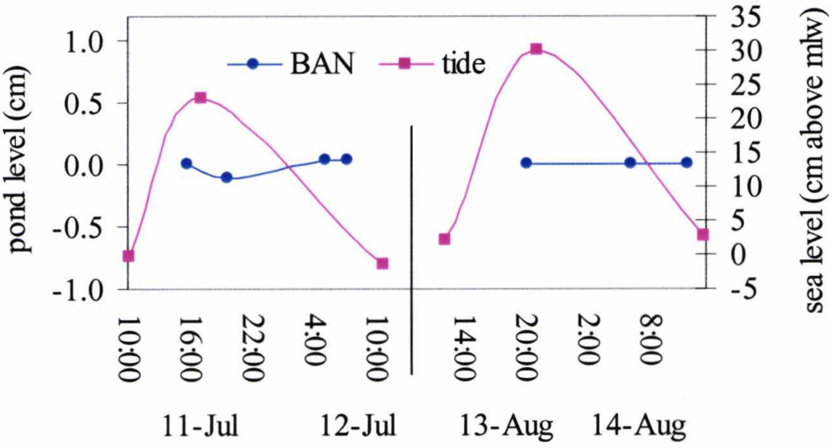
Table 4.2 Short-term rise in pond water levels. Shaded values represent records of greater than 0.2 cm, the lower limit for detecting tidal influence in ponds.

Pond	**Date**	**Rise in water level (cm)**
BAN	11 - 12 Jul, 2000*	0.13
BAN	13 - 14 Aug, 2000	0
BAN	17 - 20 Apr, 2000	0
BEL	10 Jul, 2000	0.70
BLU	14 Nov, 2001	0.08
BLU	20 Oct, 2001	0.07
BLU	27 Oct, 2001	0.32
BLU	30 - 31 Jan, 2001	1.7
BON	20 - 22 Jul, 2000	3.5
BON	21 - 22 Apr, 2000	0.26
FLA	20 - 22 Jul, 2000	0.93
FLA	21 - 22 Apr, 2000	0.51
GUA	14 - 16 Jul, 2000	0.14
GUA	19 - 20 Aug, 2000	0
GUA	30 Jul - 1 Aug, 2000	0
GUA	30 Jun - 1 Jul, 2000	0
JOS	24 - 25 Aug, 2000	0
JOS	26 - 27 Jul, 2000	0

* a short rain shower occurred at 16:30, 11 July

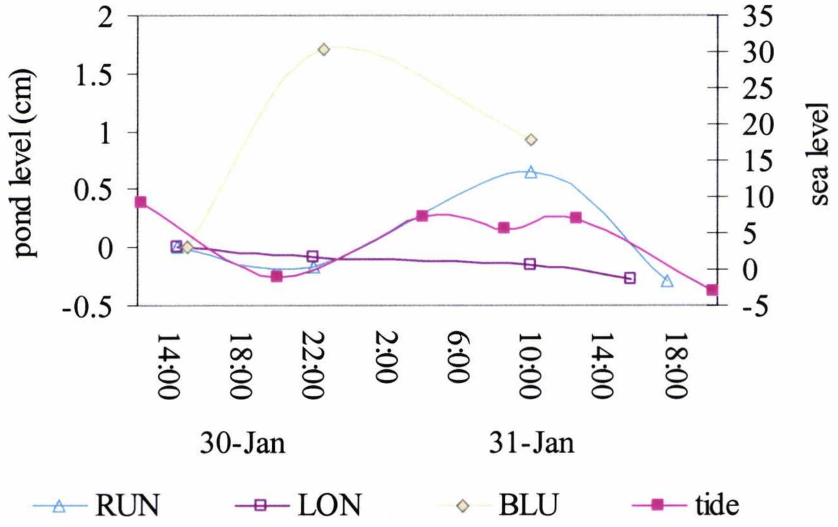
Table 4.2 (continued) Short-term rise in pond water levels. Shaded values represent records of greater than 0.2 cm, the lower limit for detecting tidal influence in ponds

Pond	Date	Rise in water level (cm)
LON	14 Nov, 2001	0.71
LON	20 Oct, 2001	1.2
LON	27 Oct, 2001	0.31
LON	30 - 31 Jan, 2001	0.15
PTP	21 - 22 Apr, 2000	0.75
RED	21 - 22 Apr, 2000	1.9
RUN	14 Nov, 2001	0.44
RUN	20 Oct, 2001	0.33
RUN	27 Oct, 2001	0.04
RUN	30 - 31 Jan, 2001	0.82
SIN	28 Jul, 2001	2.6
WB	18 - 20 Apr, 2000	0.19

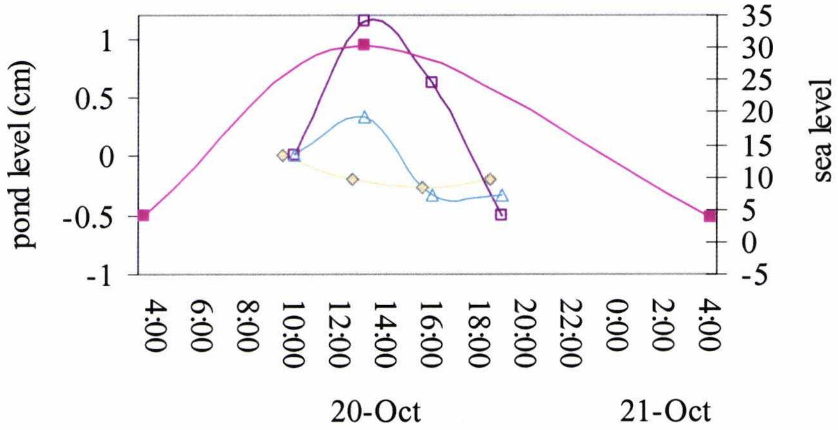


a) Water level at BAN, 11-12 July, and 13-14 August,

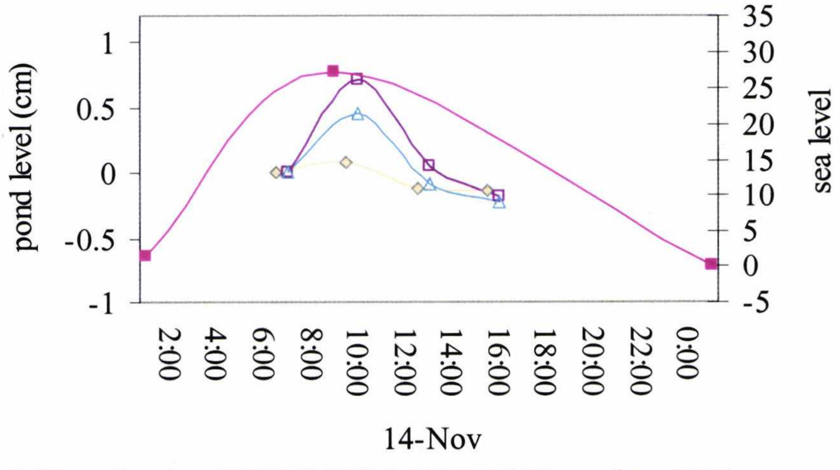
Figure 4.3 Diurnal water level fluctuations in Beef Island ponds



b) Water levels at RUN, LON & BLU, 30-31 January, 2001

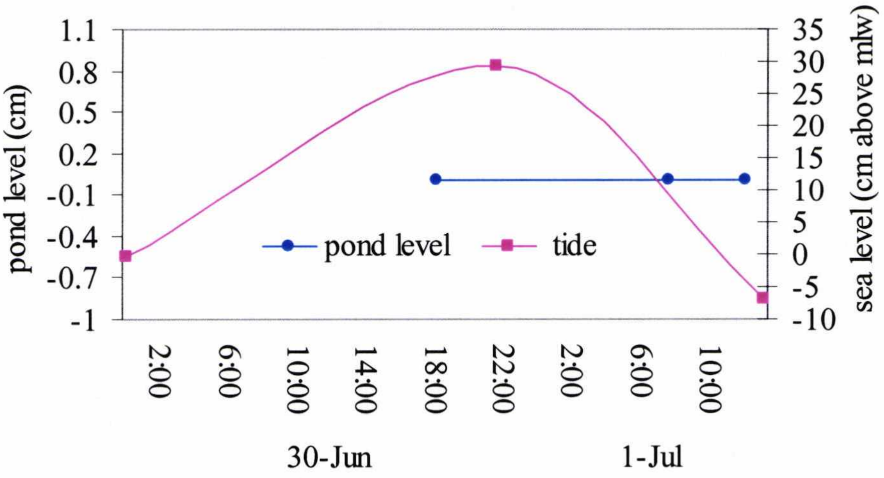


c) Water levels at RUN, LON & BLU, 20 October, 2001

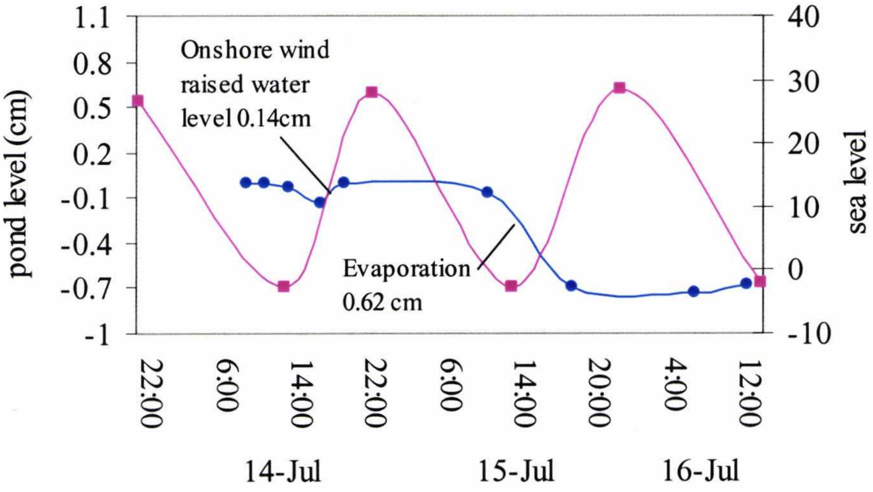


d) Water levels at RUN, LON & BLU, 14 November, 2001

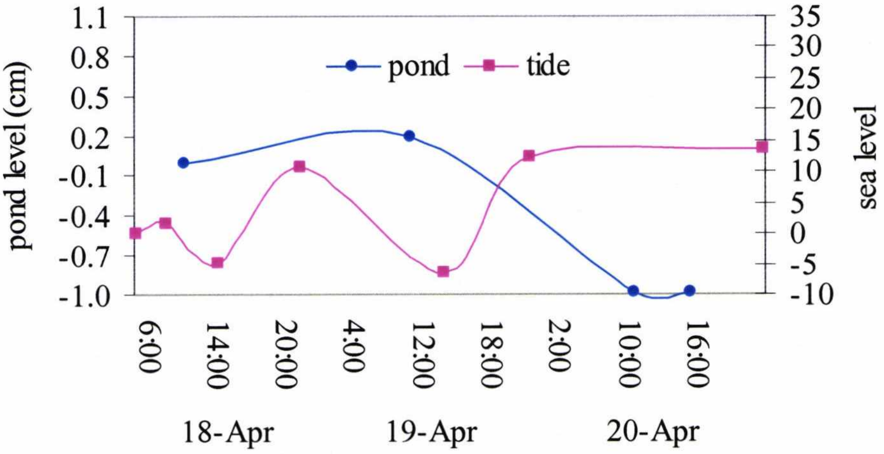
Figure 4.3 (continued) Diurnal water level fluctuations in Beef Island ponds



a) Water level at GUA, 30 June through 1 July

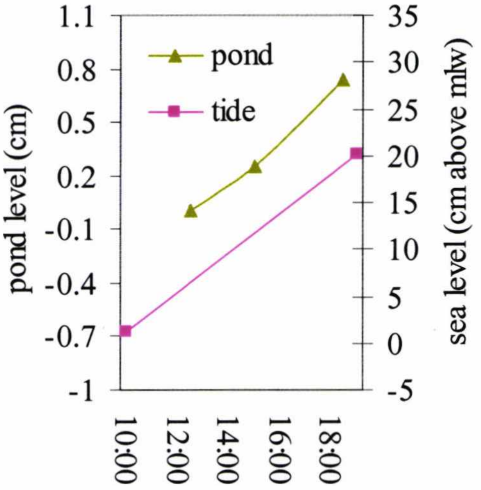


b) Water level at GUA, 14-16 July

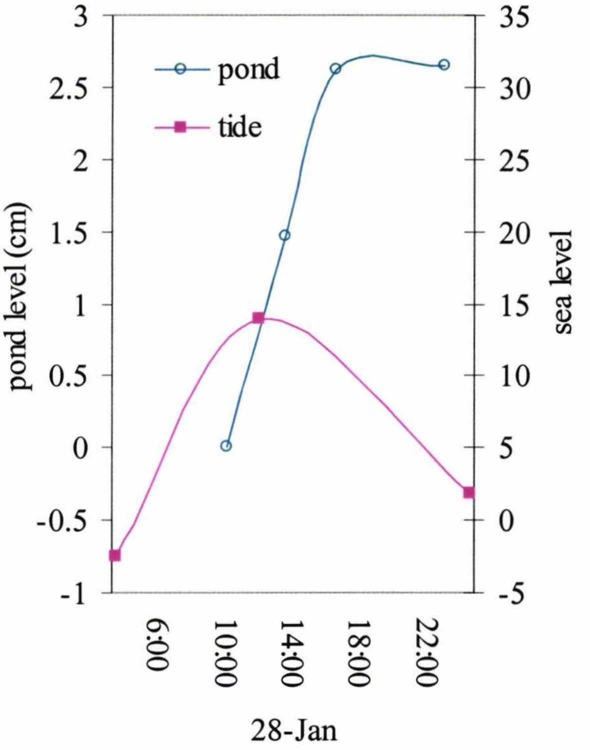


c) Water level at WB, 18-20 April

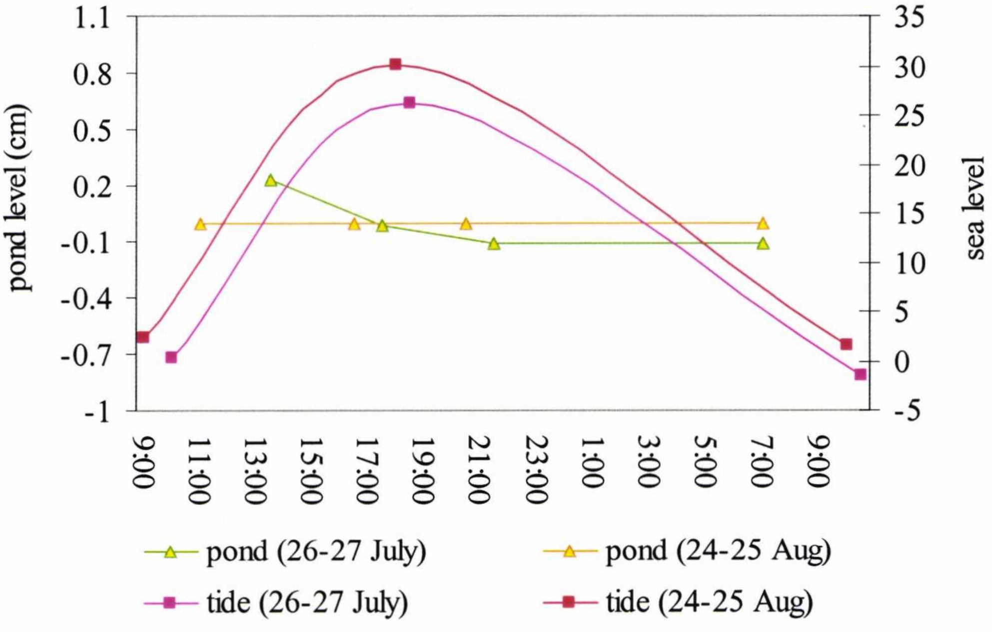
Figure 4.4 Diurnal water level fluctuations in GUA and WB



a) Water level at BEL, 10 July, 2000

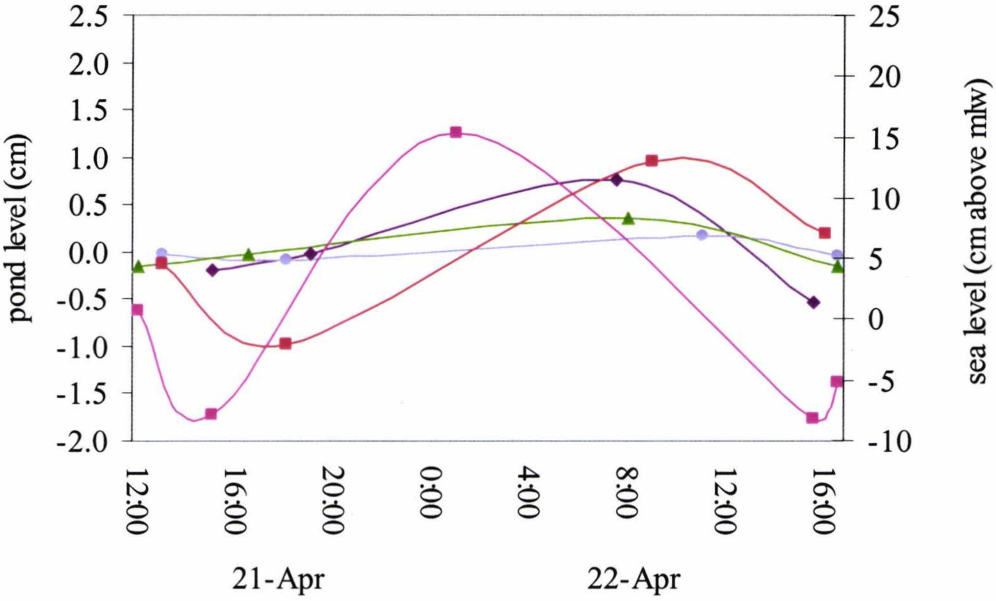


b) Water level at SIN, 28 January, 2001

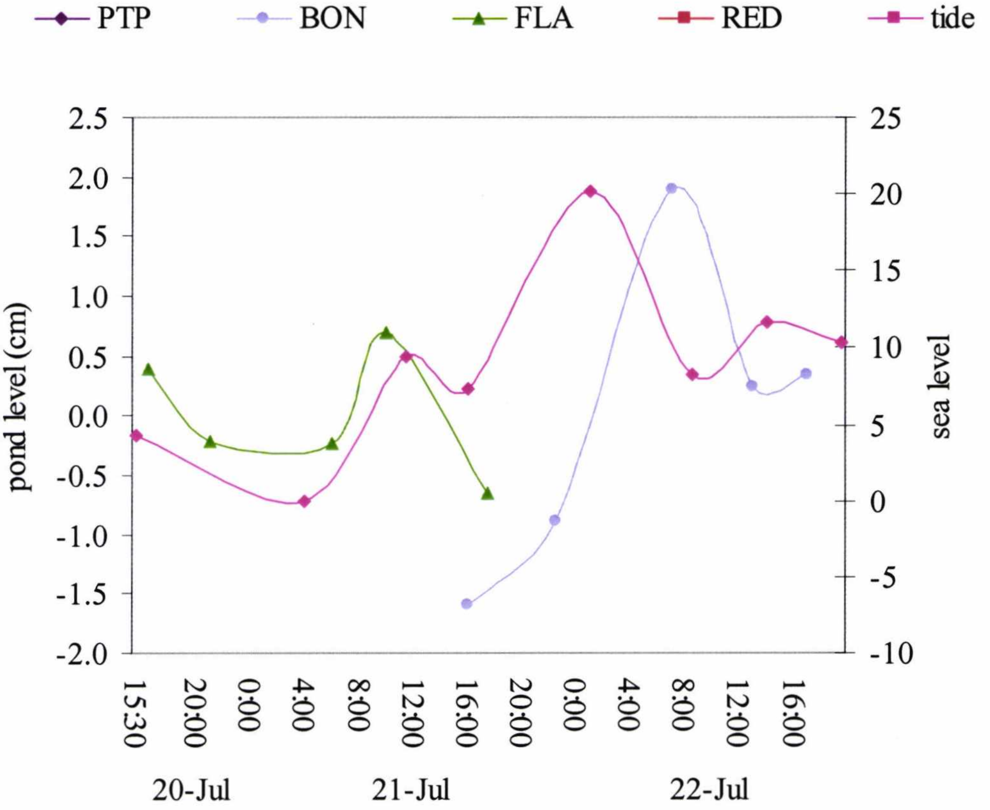


c) Water level at JOS, 26-27 July and 24-25 August, 2000

Figure 4.5 Diurnal water level fluctuations in BEL, JOS and SIN



a) 21-22 April, 2000



b) 20-22 July, 2000

Figure 4.6: Diurnal water level fluctuations in Anegada's ponds

4.2 (d) Mangrove distributions

4.2 (d.*i*) Variability among ponds

Mangrove species representation was highly variable among ponds (Table 4.3 and Figures 4.7 – 4.16). The mangrove forests around GUA and NOR (Figures 4.7 and 4.8) were monocultures of white mangrove, while buttonwood dominated the forests of LEE (Figure 4.9) and BAN (Figure 4.13). Black mangrove was dominant at BLU (Figure 4.13) and WB (Table 4.3), and red mangrove was dominant at SIN (Figure 4.11). Other ponds had mixed forests with variable species compositions. A near-equal mix of buttonwood and white mangrove occurred at SAN; white and black mangroves dominated the forest at JOS (Figure 4.15); a mix of buttonwood, white, and red mangrove occurred at BON (Figure 4.16) and BEL (Figure 4.14); buttonwood, white, and black mangrove occurred at LON (Figure 4.12); and all 4 species were well represented at HAN, RUN and FLA (Figures 4.12 and 4.16). Overall, black mangrove (35%) and white mangrove (33%) were the most common species at salt ponds, while buttonwood (20%) was less common and red mangrove (12%) was least common. The prevalence of black and white mangroves was consistent with Bossi & Cintron's (1990) characterization of basin mangrove forests in the wider Caribbean region.

4.2 (d.*ii*) Testing the relationship between mangrove distributions and pond hydrologies

The four variables defining the proportion of forest at each pond represented by each of the mangrove species (Table 4.3) were uncorrelated with one another. Correlation coefficients ranged from -0.04 between black and red mangroves to -0.40 between black and white mangroves (Table 4.4). This result suggests that the distribution of each mangrove species is not related to the distributions of other species. As such, the 4 mangrove distribution variables shown in Table 4.3 may be used as independent indicators of hydrological variation in ponds.

These variables, however, performed poorly in a Discriminant Function Analysis using mangrove distributions to group ponds according to inundation period. Only 43% of cross-validated ponds grouped correctly. Mangrove distributions performed somewhat better at grouping ponds according the degree of sea connection, in which 79% of cross-validated ponds grouped correctly. The number of ponds included in this analysis (16) was insufficient for rigorous statistical analysis because of the great variability in mangrove distributions among ponds.

Nevertheless, some inferences about the distribution of mangroves with respect to hydrological characteristics are described in the following sections.

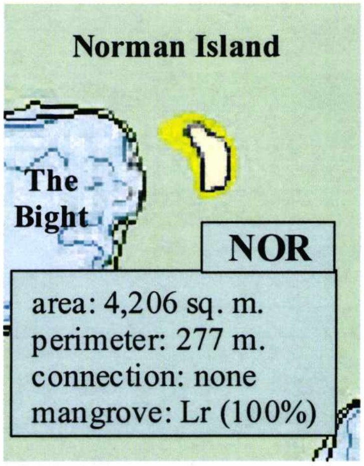
Table 4.3 Proportional representation of mangrove species, occurrence of red mangrove patches and tidal influence at each salt pond

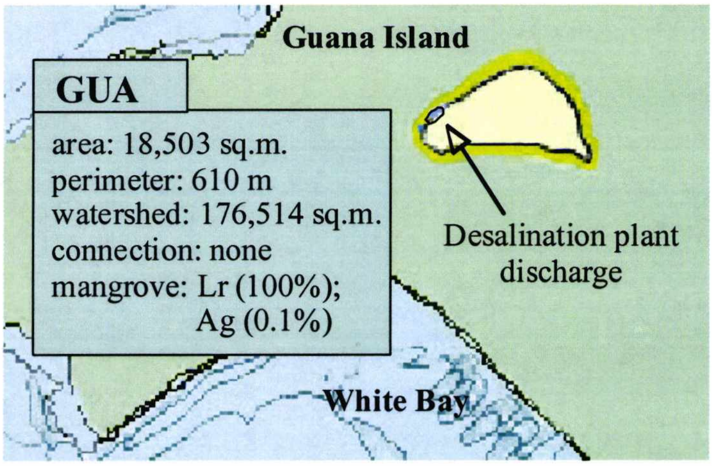
Mangrove color codes:
≥30% Black Mangrove = blue
≥30% Buttonwood = grey
≥30% Red Mangrove = red
≥30% White Mangrove = yellow
≥20% any species = bold

Pond	**Buttonwood**	**White mangr.**	**Black mangr.**	**Red mangr.**	**Patches red[1] (m^2)**	**Tidal influence**
BAN	**90%**	0%	0%	10%	0	X
BEL	11%	**58%**	0%	**31%**	1,000	b
BLU	4%	3%	**83%**	10%	1,500	b
BON	**45%**	**35%**	0%	**20%**	2,000	b
FLA	**23%**	**26%**	**40%**	11%	500	b
GUA	0%	**100%**	0%	0%	0	X
HAN	**45%**	**38%**	13%	4%	0	X
JOS	0%	**32%**	**66%**	2%	0	X
LEE	**100%**	0%	0%	0%	0	X
LON	**37%**	7%	**56%**	0%	0	b /X
NOR	0%	**100%**	0%	0%	0	X
RUN	9%	**47%**	**33%**	11%	1,000	b
SAL	0%	0%	0%	0%	0	---
SAN	**50%**	**50%**	0%	0%	0	X
SIN	0%	6%	16%	**78%**	2,000	b
WB[2]	0%	0%	**85%**	15%	---	---

[1] Area of shore forest in which red mangr. represents more than 75% of mangroves.

[2] Mangrove representation for WB was estimated by visual surveys

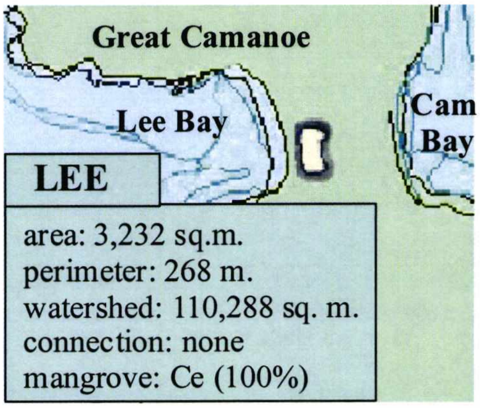


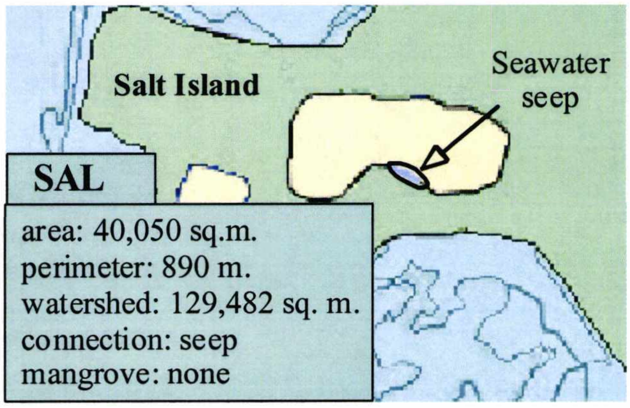


▨ **Buttonwd (Ce)** 🟨 **White Mangr (Lr)** 🟦 **Black Mangr (Ag)** 🟥 **Red Mangr (Rm)**

Figure 4.7 Mangrove distributions and hydrological characteristics of NOR

Figure 4.8 Mangrove distributions and hydrological characteristics of GUA

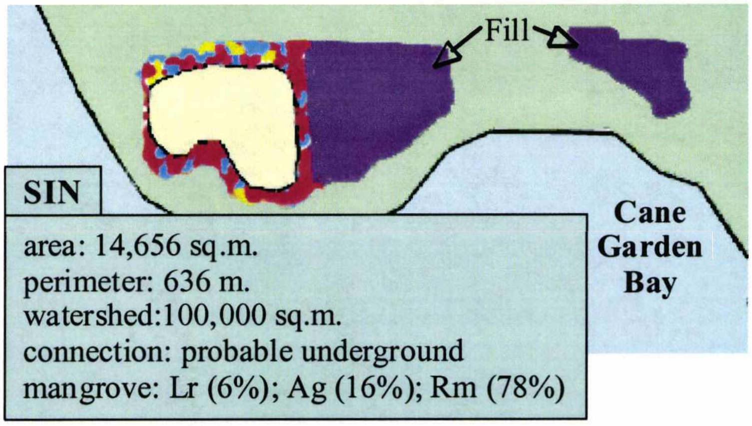




▨ **Buttonwd (Ce)** 🟨 **White Mangr (Lr)** 🟦 **Black Mangr (Ag)** 🟥 **Red Mangr (Rm)**

Figure 4.9 Mangrove distributions and hydrological characteristics of LEE

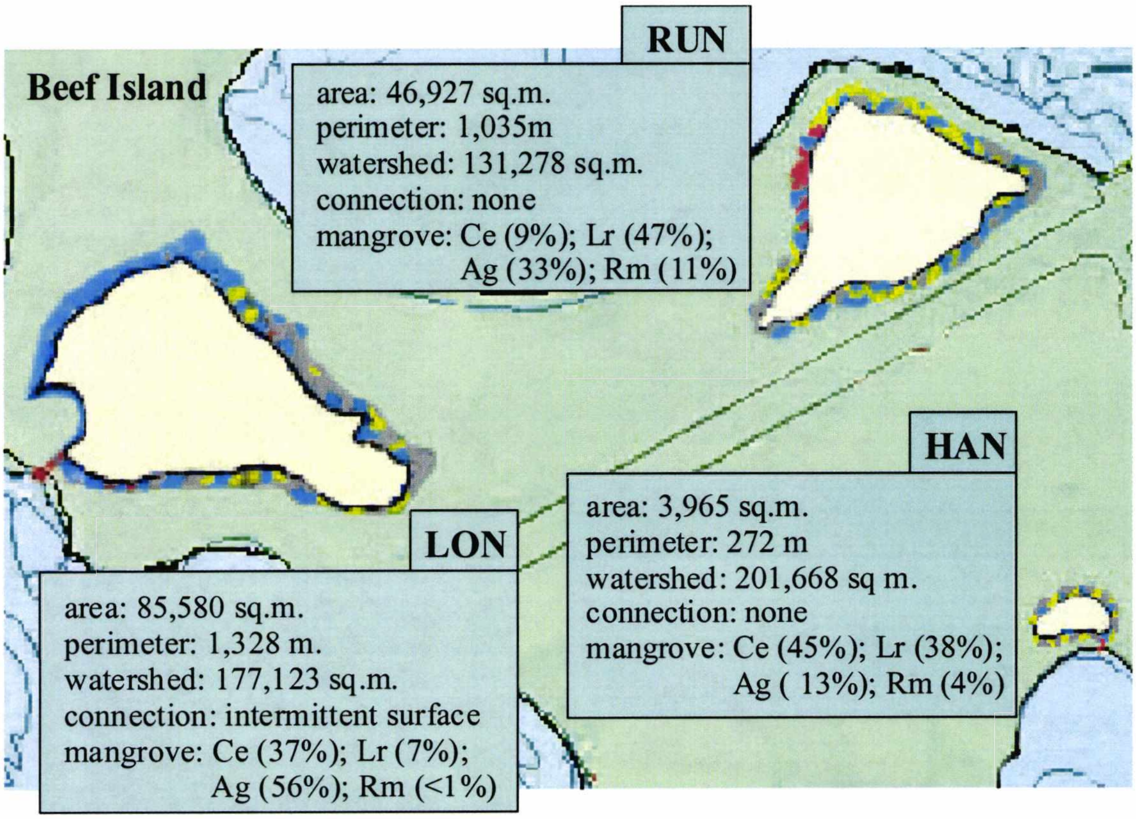
Figure 4.10 Mangrove distributions and hydrological characteristics of SAL



area: 14,656 sq.m.
perimeter: 636 m.
watershed:100,000 sq.m.
connection: probable underground
mangrove: Lr (6%); Ag (16%); Rm (78%)

▨ **Buttonwd (Ce)** 🟨 **White Mangr (Lr)** 🟦 **Black Mangr (Ag)** 🟥 **Red Mangr (Rm)**

Figure 4.11 Mangrove distributions and hydrological characteristics of SIN



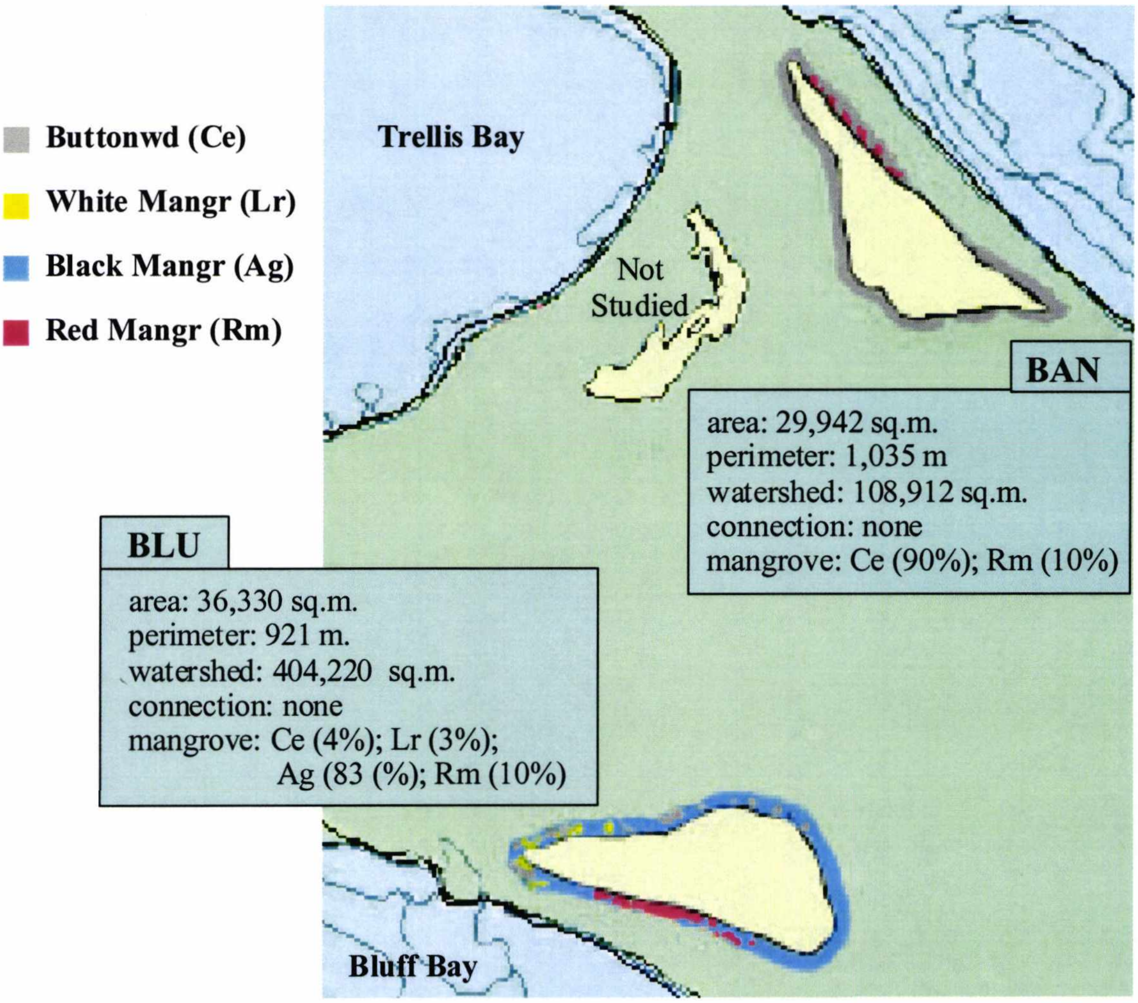
RUN
area: 46,927 sq.m.
perimeter: 1,035m
watershed: 131,278 sq.m.
connection: none
mangrove: Ce (9%); Lr (47%); Ag (33%); Rm (11%)

LON
area: 85,580 sq.m.
perimeter: 1,328 m.
watershed: 177,123 sq.m.
connection: intermittent surface
mangrove: Ce (37%); Lr (7%); Ag (56%); Rm (<1%)

HAN
area: 3,965 sq.m.
perimeter: 272 m
watershed: 201,668 sq m.
connection: none
mangrove: Ce (45%); Lr (38%); Ag (13%); Rm (4%)

▨ **Buttonwd (Ce)** 🟨 **White Mangr (Lr)** 🟦 **Black Mangr (Ag)** 🟥 **Red Mangr (Rm)**

Figure 4.12 Mangrove distributions and hydrological characteristics of the western ponds of Beef Island



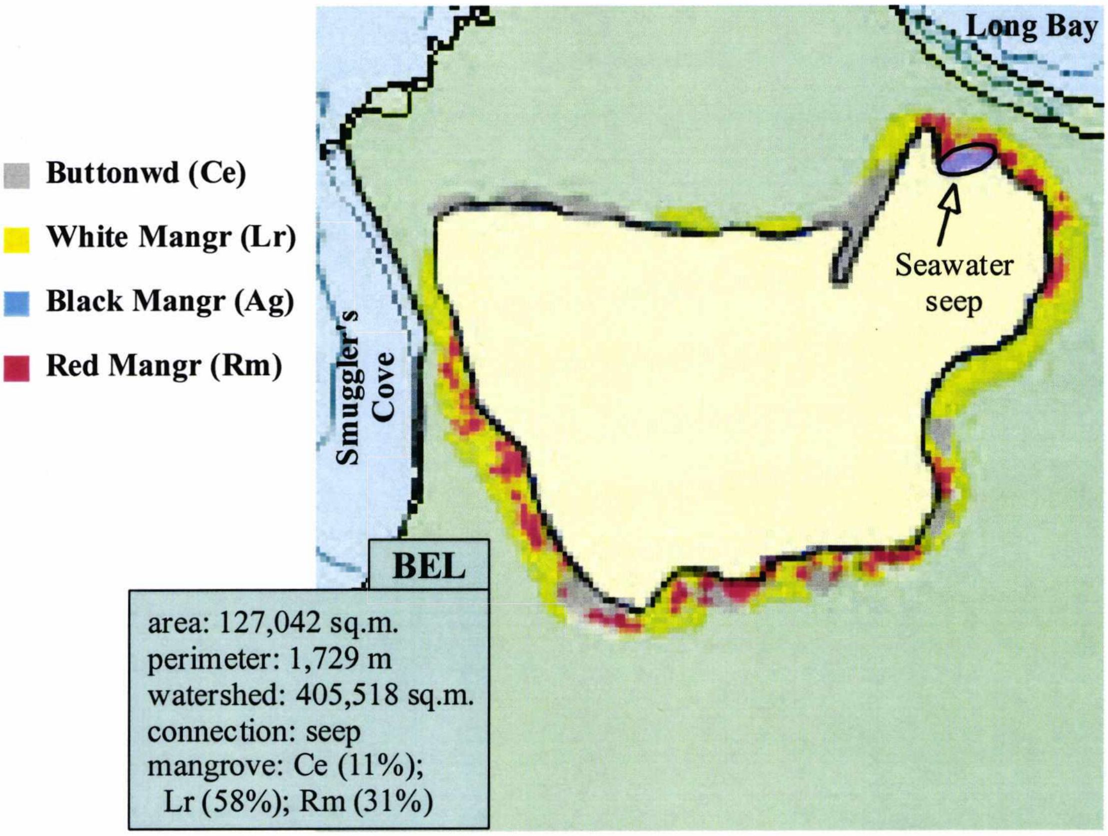
BAN

area: 29,942 sq.m.
perimeter: 1,035 m
watershed: 108,912 sq.m.
connection: none
mangrove: Ce (90%); Rm (10%)

BLU

area: 36,330 sq.m.
perimeter: 921 m.
watershed: 404,220 sq.m.
connection: none
mangrove: Ce (4%); Lr (3%);
Ag (83 (%); Rm (10%)

Figure 4.13 Mangrove distributions and hydrological characteristics of the eastern ponds of Beef Island



▨ Buttonwd (Ce)

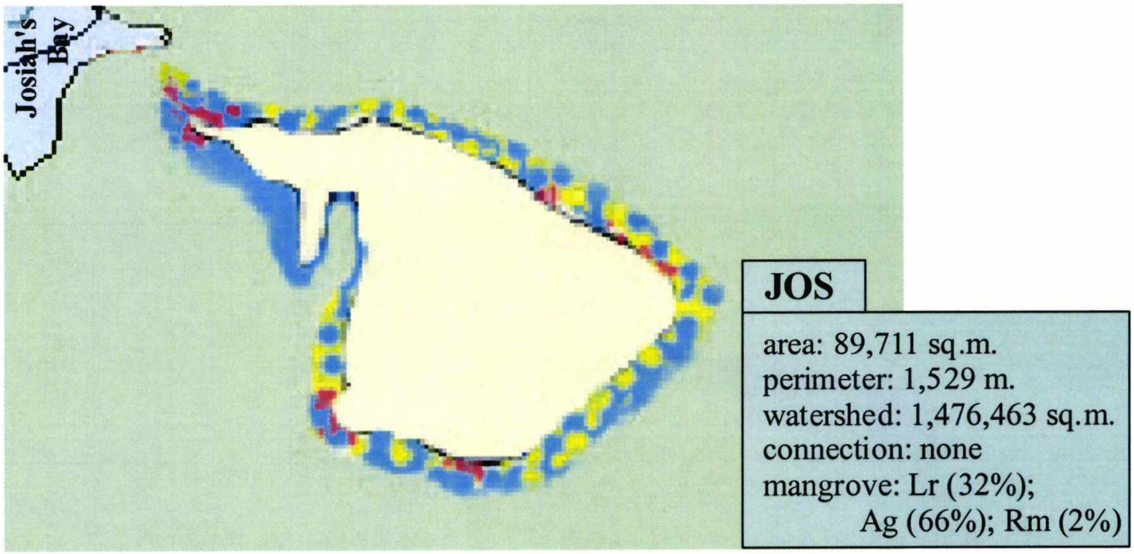
🟨 White Mangr (Lr)

🟦 Black Mangr (Ag)

🟥 Red Mangr (Rm)

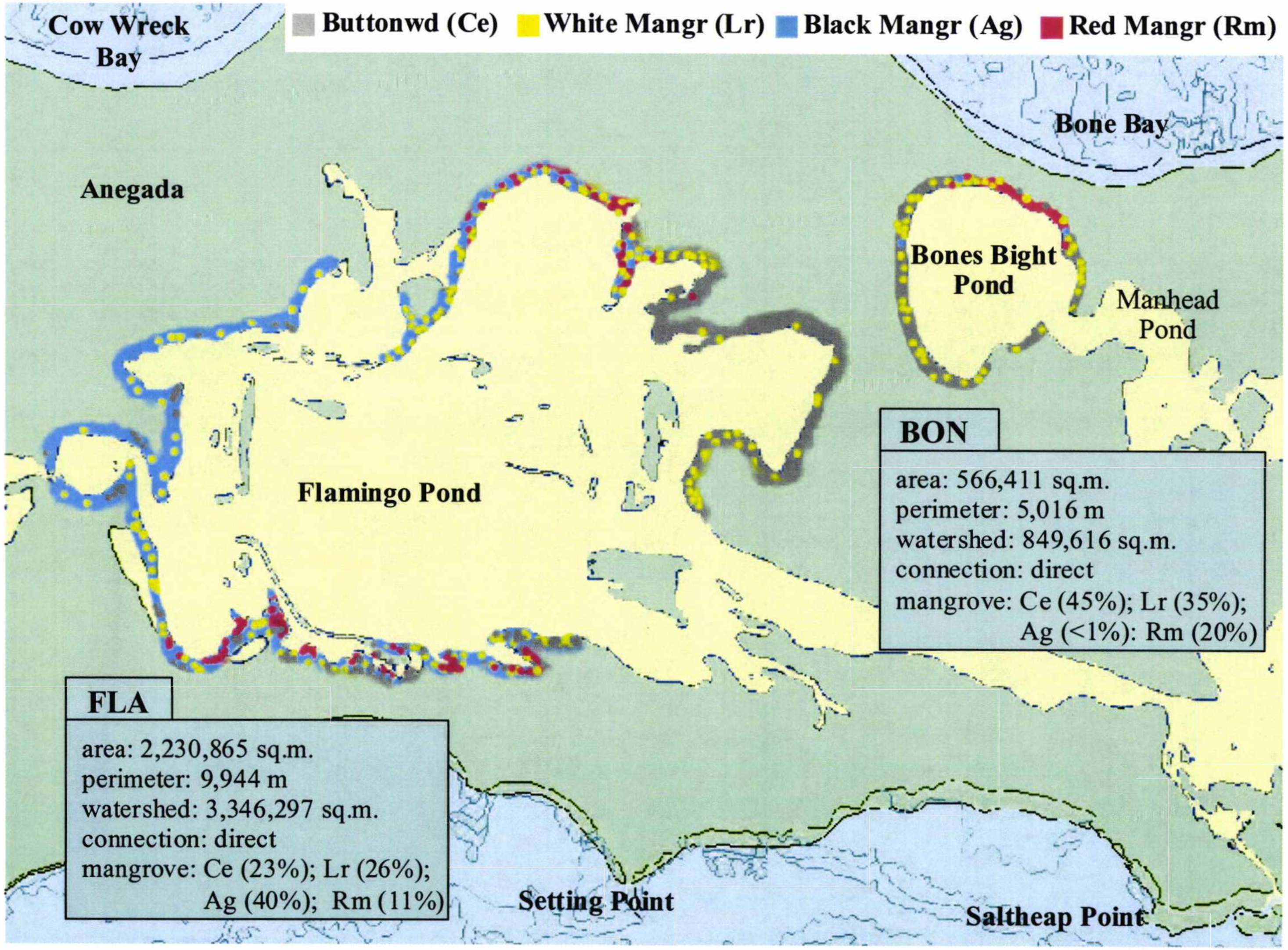
area: 127,042 sq.m.
perimeter: 1,729 m
watershed: 405,518 sq.m.
connection: seep
mangrove: Ce (11%);
Lr (58%); Rm (31%)

Figure 4.14 Mangrove distributions and hydrological characteristics of BEL



area: 89,711 sq.m.
perimeter: 1,529 m.
watershed: 1,476,463 sq.m.
connection: none
mangrove: Lr (32%);
Ag (66%); Rm (2%)

Figure 4.15 Mangrove distributions and hydrological characteristics of JOS



BON

area: 566,411 sq.m.
perimeter: 5,016 m
watershed: 849,616 sq.m.
connection: direct
mangrove: Ce (45%); Lr (35%); Ag (<1%): Rm (20%)

FLA

area: 2,230,865 sq.m.
perimeter: 9,944 m
watershed: 3,346,297 sq.m.
connection: direct
mangrove: Ce (23%); Lr (26%); Ag (40%); Rm (11%)

Figure 4.16 Mangrove distributions and hydrological characteristics of FLA and BON

Table 4.4 Correlations between the proportions of mangrove species represented at ponds

	White mangrove	Black mangrove	Red mangrove
Buttonwood	-0.32	-0.38	-0.23
White mangrove		-0.40	-0.20
Black mangrove			-0.04

4.2 (d.*iii*) Distribution patterns

White mangrove and buttonwood were dominant at small non-permanent ponds relatively distant from the sea (e.g. LEE, NOR and SAN: Table 4.1 and 4.3). These ponds had wide, sandy berms that were covered with dry forest vegetation. Bottom sediments were sandy and comparatively well drained. The prevalence of white mangrove and buttonwood at such ponds was consistent with expectation, since these species normally occur in drier areas than black or red mangroves (Imbert *et al.* 2000; Lewis 1990). These species, however, were by no means restricted to ponds that were well isolated from the sea. Mangrove distributions within individual ponds that supported mixed forests were often patchy and appeared to follow small-scale variations in geomorphology, such as sediment type, shore slope, and berm structure.

Buttonwood was generally concentrated along sloped areas of shoreline where hillsides bordered part of a pond shore. The elevated shoreline in these areas protected these mangroves from waterlogging and high salinity. Surprisingly, though, buttonwood also occurred in association with red and black mangroves, which normally grow under inundated soil conditions (Imbert *et al.* 2000; Lewis 1990; Lugo & Snedaker 1974). Black and/or white mangrove were abundant throughout most ponds, but white mangrove never grew in submerged areas. In fact, 5 years after the onset of desalination plant discharge that maintained inundation and prevented normal drying and filling cycles at GUA, the white mangroves nearest the shore perished. New white mangroves trees grew just behind the original stand of mangroves. White mangroves from the original stand that survived permanent inundation grew small pneumatophores, which aid in root respiration.

4.2 (d.*iv*) Patches of red mangroves are indicative of tidal influence

Despite its low abundance at ponds, red mangrove were situated in dense patches of 500 to 2,000 m^2 along the shoreline. These patches occurred on the seaward sides of ponds in areas where the shore slope was near zero and sediments were composed of soft organic mud (e.g. RUN, BLU and BON, Figures 4.12, 4.13 and 4.16, respectively). They were always separated from seashore mangroves by an elevated berm. These red mangrove patches were intriguing in light of the fact that this species normally grows with its roots immersed in seawater and is not tolerant of hypersalinity (Lugo & Snedaker 1974).

The occurrence of red mangrove patches was highly correlated (0.87) with tidal influence (Table 4.3). These patches were defined as forested shoreline areas of at least 500 m^2 in which red mangrove represented more than 75% of mangroves. The same correlation, however, was found using a less stringent definition, requiring only 50% representation of red mangrove in a patch. The only exception was LON (Figure 4.12), which did not have red mangrove patches but sometimes experienced tidal fluctuations because it was connected with the sea. These results suggest that patches of red mangrove occur in areas of lower salinity soil, perhaps where there is underground communication with the sea.

Red mangrove was the dominant mangrove at only one pond, SIN, where it grew densely around 75% of the shore (Figure 4.11). Tide-driven water level rise in SIN was 1.5 times the greatest water level rise measured in any other unconnected pond (Table 4.2). These observations suggest that a high level of seawater exchange occurred through the coral berm that separated SIN from the sea.

4.2 (d.*v*) Inferences from mangrove distributions

The variable distribution of mangroves observed among BVI salt ponds is not unique, despite the well-documented zonation patterns of Caribbean mangroves (Ellison & Farnsworth 1993; Lugo & Snedaker 1974). Thomas *et al.* (1992) found differences in mangrove species composition in the forests around several seawater ponds in Bermuda. Bacon (1994) observed that red mangrove, in particular, occurs in a range of habitats, from coastal fringes to hypersaline basins. Lugo & Snedaker (1974) also pointed out that mangrove zonation patterns were not consistent in large areas of flat land. Such topography is typical of hypersaline basins.

Bacon (1994) claimed that the variable distribution of mangroves in some areas indicates that mangroves do not show high fidelity to particular habitats. The data presented here suggest an alternative explanation—that mangroves, being highly specialized to particular edaphic conditions, are distributed according to highly localized hydrological variations within and among hypersaline basins. This conclusion supports Lee's (1999) suggestion that future research on the connectivity between mangroves and the sea should be done at smaller spatial scales than used in previous studies.

This chapter described hydrological variation among ponds and patterns of mangrove distribution. Hydrology controls water chemistry, which is explored in the following chapter.

Chapter 5: Water Chemistry

5.1 Introduction

Salinity is not only a defining characteristic of salt ponds, but it is also considered to be one of the most important biological stressors in these ecosystems (Carpelan 1967; Colburn 1988; Garcia & Niell 1993; Garcia-Pichel *et al.* 1999; Pinckney *et al.* 1995). Salinity fluctuates widely in shallow hypersaline water bodies because their high surface to volume ratio makes them especially sensitive to seasonal and shorter-term environmental changes (Carpelan 1967; Garcia & Niell 1993). Weather patterns control the concentration of salts by evaporation and dilution (Blinn 1971; Carpelan 1957; Kjerfve *et al.* 1996; Pinckney *et al.* 1995; Savenije 1988; Watts *et al.* 2001). Seawater input and flushing in some coastal ponds also influence salinity (Carpelan 1967; Hudec & Sonnenfeld 1980; Kjerve *et al.* 1996; Meshal 1987; Thomas *et al.* 1991; Victor *et al.* 1997). Salinity stratification is prevented by wind mixing in shallow ponds (Blinn 1971; Kjerfve *et al.* 1996; Kristensen & Hulsher-Emeis 1972; Victor *et al.* 1997), though salinity and temperature stratification are characteristic of deeper hypersaline water bodies (Borowitzka 1981; Hudec & Sonnenfeld 1980; Meshal 1987; Watts *et al.* 2001). Oxygen concentrations, temperature and pH co-vary with salinity and each contributes to the physiologically extreme conditions typical of hypersaline water bodies (Bayly 1972; Borowitzka 1981; Britton & Johnson 1987; Carpelan 1967; Garcia-Pichel *et al.* 1999; Greenwald & Hurlbert 1993; Gunter 1967; Larsen 1980; Williams 1998).

Dissolved oxygen has been shown to vary not only with salinity and temperature but also with insolation, depth and composition of the photosynthetic community (Burke 1995; Burke & Knott 1997; Carpelan 1957; Copeland 1967; Lonzarich & Smith 1997; Pinckney & Paerl 1997). Oxygen supersaturation, resulting from photosynthetic activity, has been reported for hypersaline producer communities, including phytoplankton (Copeland 1967; Pedros-Alio *et al.* 2000), benthic microbial mats (Burke & Knott 1997; Cornee *et al.* 1992; Pinckney & Paerl 1997) and beds of wigeongrass, *Ruppia maritima* (Kantrud 1991). Dissolved oxygen in these communities can be depleted by respiration at night (Burke 1995; Burke & Knott 1997; Canfield & Des Marais 1994; Copeland 1967; Lonzarich & Smith 1997).

Hypersaline communities may also be limited by nutrient availability (Borowitzka 1981; Burke & Knott 1997; Davis 1978; Javor 1983; Nixon 1970), but some studies have shown that nutrient concentrations in coastal hypersaline water bodies may be elevated with respect to marine waters (Carpelan 1957; Comin *et al.* 1999; Kristensen 1964; Pedros-Alio *et al.* 2000; Shyka & Sebens 2000; Victor *et al.* 1997).

The purpose of this chapter is to describe the relationship between salinity variation and hydrological variation and to provide a baseline description of biologically important chemical and physical characteristics of hypersaline waters in BVI salt ponds.

5.2 Results and discussion

All records of salinity, water temperature, pH, turbidity and dissolved oxygen recorded during this study are detailed in Appendix B. These data are summarized in Table 5.1.

Table 5.1 Chemical characteristics of salt ponds: salinity, water temperature, pH, turbidity and dissolved oxygen concentration.
Values are shown as $\overline{x} \pm \sigma$ (N).

Pond	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	[O2] (mg/L)
BAN	100 ± 49 (26)	32 ± 5.1 (26)	8.4 ± 0.2 (12)	36 ± 17 (15)	4.1 ± 2.4 (20)
BEL	150 ± 92 (20)	34 ± 4.1 (15)	7.3 ± 0.4 (3)	35 ± 17 (4)	2.3 ± 2.4 (14)
BLU	72 ± 32 (3)	---	---	---	---
BON	86 ± 21 (15)	32 ± 2.2 (13)	8.3 ± 0.1 (3)	27 ± 16 (4)	4.6 ± 1.3 (11)
FLA	100 ± 29 (16)	32 ± 2.0 (15)	8.0 ± 0.2 (3)	38 ± 27 (4)	4.1 ± 1.8 (12)
GUA	74 ± 27 (20)	31 ± 4.8 (18)	8.4 ± 0.2 (7)	45 ± 35 (13)	7.0 ± 2.9 (16)
JOS	52 ± 33 (19)	30 ± 7.3 (15)	8.4 ± 0.8 (9)	55 ± 67 (11)	9.1 ± 4.7 (11)
LON	65 ± 30 (8)	22 ± 7.6 (3)	8.8 ± 0.4 (8)	12 ± 5 (8)	5.9 ± 2.3 (4)
PTP	87 ± 31 (13)	32 ± 2.4 (12)	---	10 ± 4 (2)	4.4 ± 1.8 (4)
RED	160 ± 69 (15)	33 ± 3.2 (13)	8.6 (1)	110 ± 160 (3)	2.3 ± 2.3 (12)
RUN	84 ± 27 (4)	---	---	---	---
SAL	320 ± 88 (12)	38 ± 3.6 (11)	7.1 (1)	7 ± 9 (2)	0.2 ± 0.5 (9)
SIN	44 ± 8 (3)	31 ± 4.0 (2)	7.9 ± 0.1 (2)	32 ± 3 (2)	5.2 (1)
WB	53 ± 18 (13)	34 ± 2.3 (12)	---	4 ± 3 (2)	7.6 ± 4.3 (9)

5.2 (a) Salinity and its relationship with hydrology

Salinity fluctuated widely within ponds and mean salinities differed among ponds (Table 5.1 and Figure 5.1). Six of 11 ponds that were sampled more than 5 times had mean salinities below 90 ppt, and maximum salinities recorded in these ponds never exceeded 140 ppt. Mean salinities in the remaining 5 ponds were more than 100 ppt. Three of these ponds had mean salinities greater than 150 ppt, maximum salinities in excess of 250 ppt, and annual salinity fluctuations greater than 200 ppt (see Appendix B).

JOS was the only pond that regularly became hyposaline, and this occurred only after heavy rainstorms. The low salinity in JOS resulted from its large catchment area and a lack of seawater influence (see Section 4.2 (a.*i*)). Mean salinity in WB (53 ppt) was nearly equal to that of JOS, but hyposalinity did not occur. This pattern reflected a greater relative influence of seawater in WB, via a periodic sea connection (Section 4.2 (a.*ii*)) and a lesser influence of runoff water due to WB's smaller catchment area (Table 4.1).

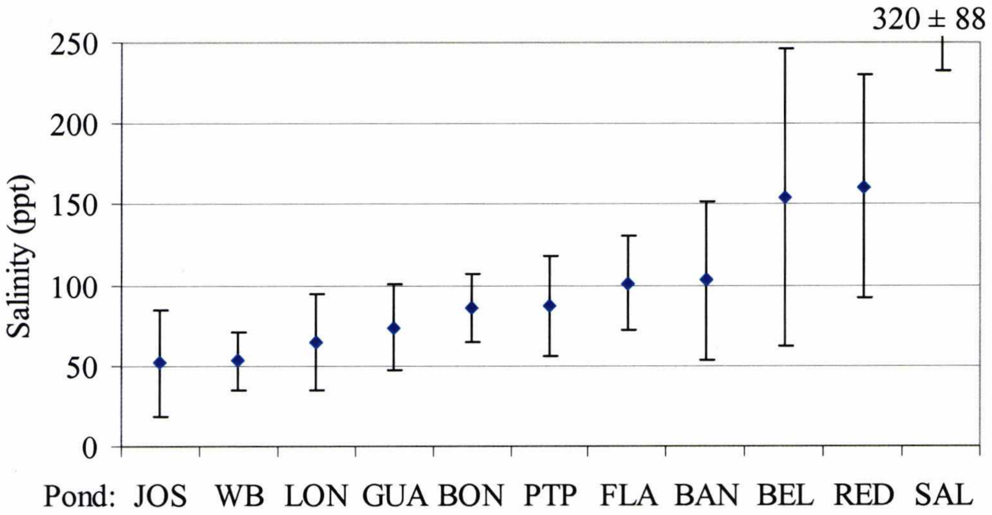


Figure 5.1 Mean pond salinities. Error bars indicate one standard deviation above and below the mean. Ponds with fewer than 5 samples are not shown.

Highly saline conditions were found in completely enclosed ponds with seawater seeps, BEL and SAL. These seeps continually supplied salts without introducing sufficient water to cause flushing. SAL was the only pond that regularly produced crystallized sodium chloride. Temporary calcite/gypsum crusts formed in BEL under highly saline conditions. RED was also a highly saline pond, and most of its bottom was covered with a precipitated calcite/gypsum pavement.

Figure 5.2 shows seasonal salinity variation in 10 ponds during 1995. Salinity in all ponds increased during the dry season, from February through August, and declined during the wet season, from September to January. Dilution by rainfall was common to all ponds but was less apparent in those connected with the sea (the Anegada ponds,Figure 5.2(c)). Its effect was greatest and most abrupt after heavy rainfall (e.g. hurricanes during September).

Despite the buffering effects of seawater exchange, salinity increased in the Anegada ponds during the beginning of the dry season (Figure 5.2(c)). This suggests that seawater entering the channel to the Anegada ponds does not flush concentrated waters out of the ponds. The phenomenon of hypersalinity despite communication with the sea has also been described in a Brazilian lagoon (Kjerfve *et al.* 1996) and in a Saudi Arabian lagoon (Meshal 1987).

5.2 (a.*i*) Dilution

Figure 5.3(a) shows the salinity response in BAN to Hurricanes Luis (September 4th, 1995) and Marilyn (September 15th, 1995) and to Hurricane Georges (September 21st, 1998) and a subsequent rainstorm (October 21st, 1998). Hurricane Luis brought 7.0 cm of rain over 2 days, and the salinity of BAN fell from 120 ppt to 76 ppt, an abrupt 37% decline in salinity. Ten days later, a further 13 cm of rain fell during Hurricane Marilyn. This second hurricane caused salinity to drop from 78 ppt to 60 ppt, a further 23% decrease. Over the following 2 months, the salinity slowly increased to 87 ppt.

In 1998, 6.5 cm of rain from Hurricane Georges diluted the salinity of BAN by 23%, from 83 to 64 ppt. Salinity gradually increased to 71 ppt by October 14th, but another 12 cm of rain fell between October 21st and 23rd and caused a further 15% dilution to 60 ppt. Continued rainfall through the following month maintained relatively low salinity in this pond.

Similar effects were seen in 3 other ponds monitored during Hurricane Georges (Figure 5.3(b)). Salinity in GUA dropped by 27%, from 83 to 61 ppt; salinity in JOS dropped by 65%, from 72 ppt to 25 ppt; and salinity in LON dropped by 67%, from 130 ppt to 43 ppt. After Hurricane Georges, salinity in these ponds gradually increased until the October 21st rains, which diluted GUA by 34%, from 62 to 41 ppt, diluted JOS by 73%, from 45 to 12 ppt, and diluted LON by 21%, from 63 to 50 ppt.

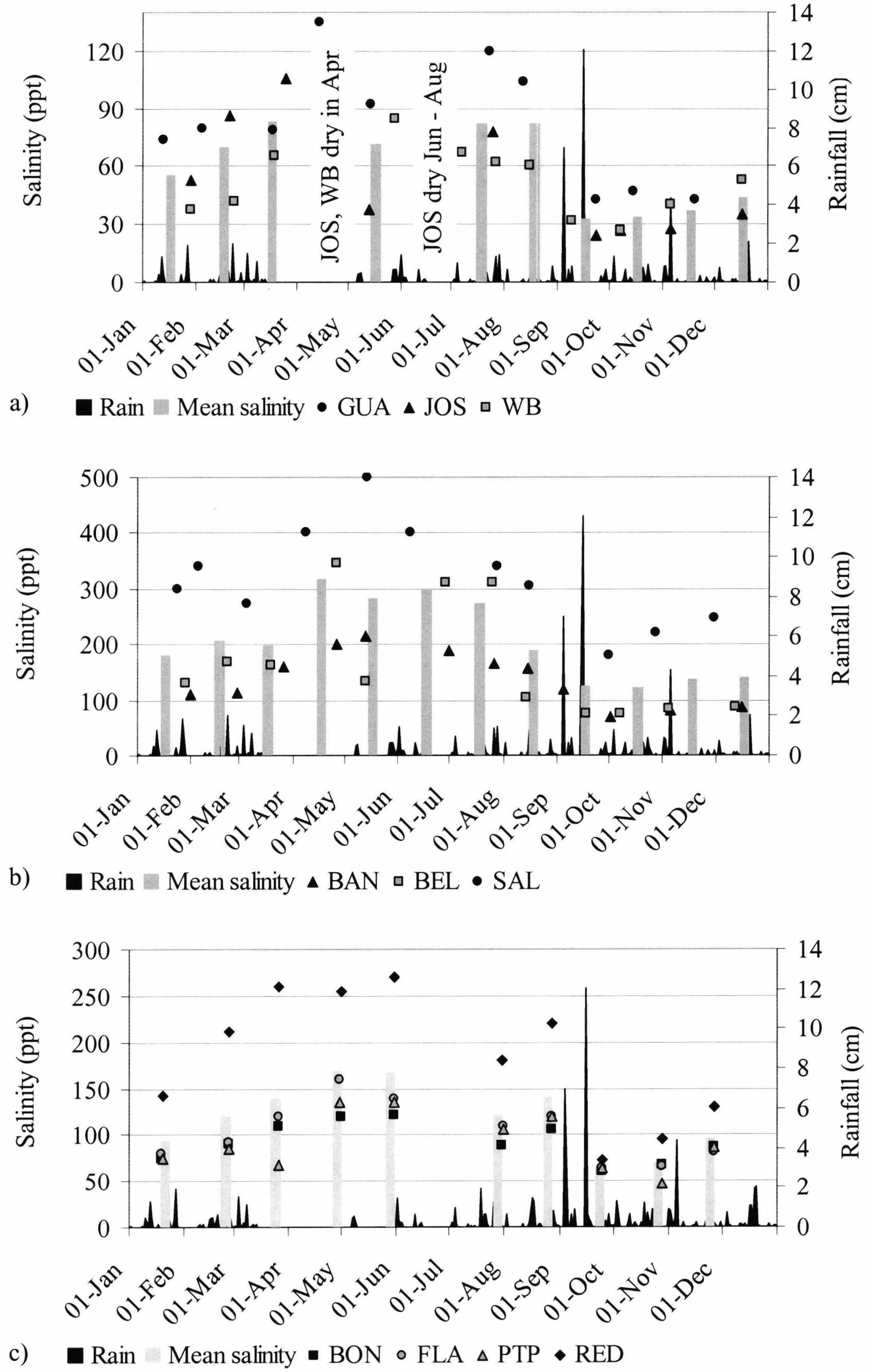
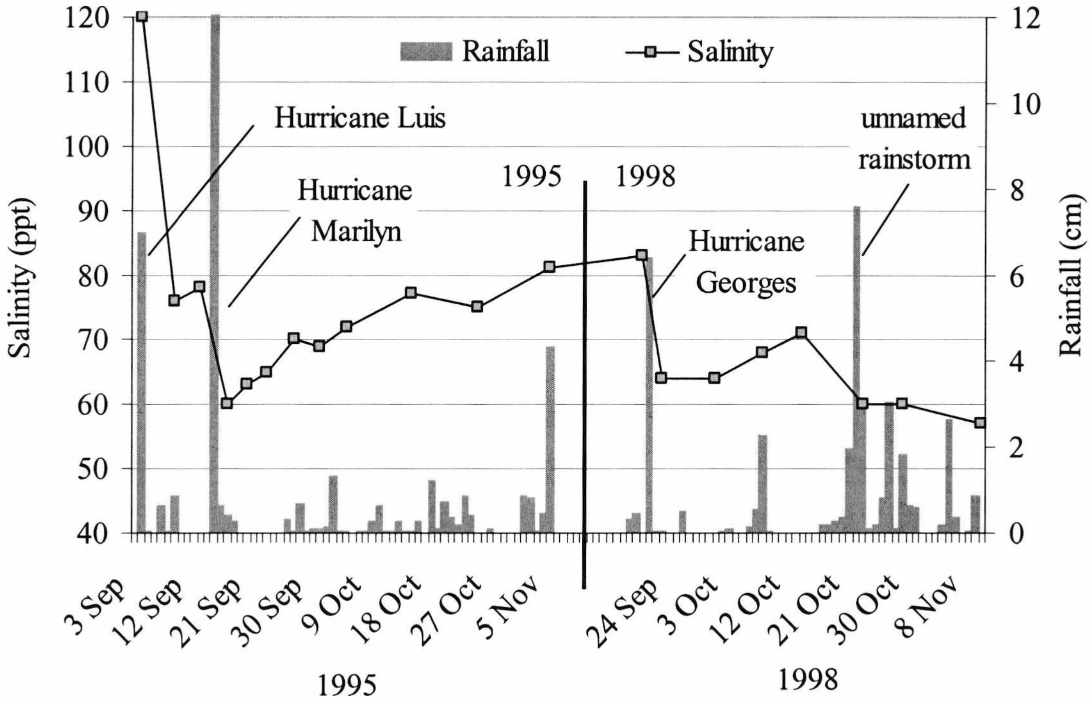
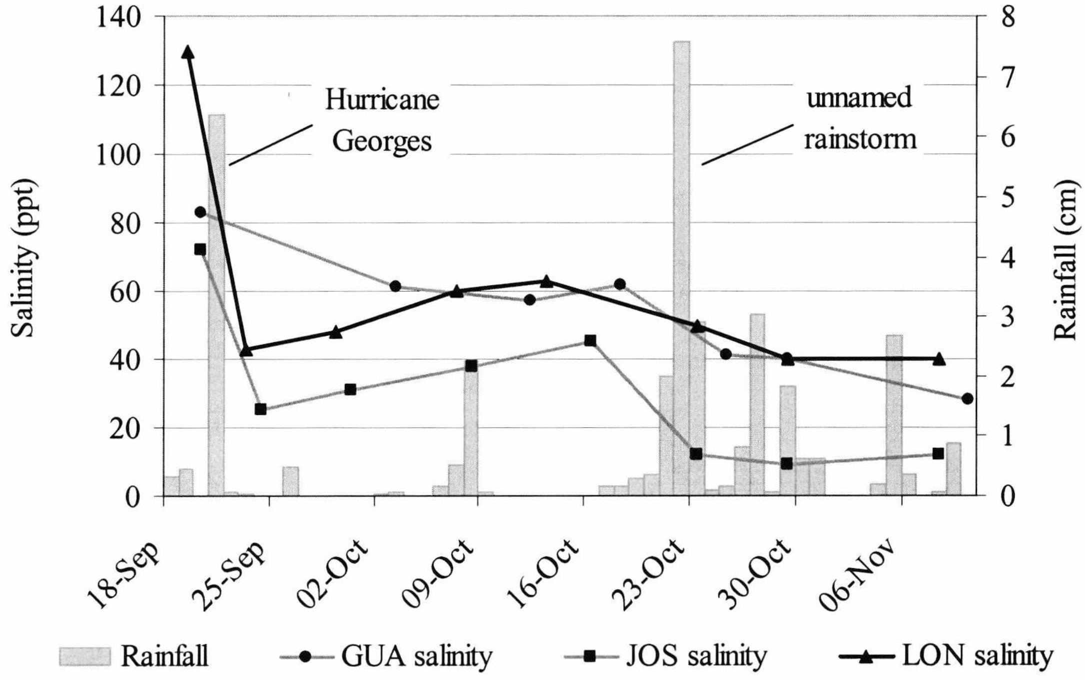


Figure 5.2 Rainfall and salinity fluctuations, 10 ponds, 1995



(a) BAN



(b) GUA, JOS and LON

Figure 5.3 Salinity responses to hurricanes and other heavy rains

The differences in the dilution effects of the 1998 rainstorms in JOS, LON and GUA (Figure 5.3(b)) can be explained by differences in pond hydrologies. The marked salinity decrease in LON seen immediately after Hurricane Georges was due to a high storm swell, which entered the pond through culverts (see Section 4.2 (a.*ii*)) and flushed the pond with seawater. Subsequent rains were not associated with high seas, and the dilution effect of these rains in LON was far less than that of the hurricane. In contrast, the dilution effects of the hurricane and the October 21st rainstorm were similar to one another in GUA and in JOS, both of which remained isolated from the sea during the hurricane. Salinity fluctuations in GUA were buffered by the regular input of seawater from a desalination plant (see Section 4.2 (a.*i*)), resulting in relatively small dilution effects from rainfall. The dilution effect of rainfall was greater in JOS than in any other pond because JOS is fed by an exceptionally large watershed (see Table 4.1).

5.2 (a.*ii*) Concentration by evaporation

Evaporation had the opposite effect of rainfall and occurred in all ponds during dry weather. Salinity and depth changes during a drought from 14 March, 1995, to 6 May, 1995, from which long-term evaporation rates (m^3 H_2O/day-ha) were calculated, are shown in Table 5.2. The maximum depth change measured was – 0.5 cm/day. This value is similar to the rate of evaporation (0.6 cm/day) reported for a hypersaline lagoon in the Red Sea (Meshal 1987).

An estimate for overall evaporation rate in ponds was calculated from long- and short-term depth measurements in BAN and JOS because these ponds were completely isolated from seawater influence (see Section 4.2 (a.*i*) and (a.*iii*)). The rate of long-term evaporation in BAN was 32 m^3 H_2O/day-ha, and the corresponding salinity increase was 1.4 ppt/day (Table 5.2(a)). Short-term evaporation rate measured in BAN during April, 2000 (45 and 32 m^3 H_2O/day-ha, Table 5.2(b)), which included daytime and nighttime hours as well as a clear day and a cloudy day, corresponded well with the long-term evaporation rate measured during April, 1995. Short-term evaporation measured during the day in JOS was very high in April (150 m^3 H_2O/day-ha, Table 5.2(b)) and in July (140 m^3 H_2O/day-ha). Evaporation during evening hours on July 26th, 2000, was lower (54 m^3 H_2O/day-ha), and during the night no evaporation occurred (Table 5.2(b)). Mean evaporation rate in JOS, including day and night hours on 26 – 27 July, was 45 m^3 H_2O/day-ha, and this figure was comparable with evaporation rates measured in BAN. Long-term and short-term methods of measuring evaporation yielded similar results, both indicating that the mean evaporation rates in ponds during dry weather was between 32 and 45 m^3 H_2O/day-ha, all (or nearly all) of which occurs during daylight. The modal evaporation rate—39 m^3 H_2O/day-ha —was used to compare evaporation in other ponds as follows.

SAL showed the greatest salinity increase (3.2 ppt/day) but the lowest volume of water loss (13 m^3 H_2O/day-ha) during the 1995 drought period (Table 5.2(a)). This apparent contradiction may be explained by the seawater seep that feeds SAL. Constant low-volume seawater input buffered depth reduction but increased salinity via the addition of salts. The rate of seawater input through the seep was estimated using the modal evaporation rate as a reference point for expected water loss. Measured loss of water in SAL was 26 m^3 H_2O/day-ha less than the expected evaporation rate of 39 m^3 H_2O/day-ha. This difference represents a total volume of 104 m^3 H_2O/day (the area of SAL is 4 ha.), which should have been lost by evaporation but was not observed in depth change. 100 m^3/day should therefore be a reasonable estimate of the rate of seawater input from the seep, which reduced the expected depth change between March and May, 1995, at SAL.

BEL, which also had a natural seawater seep, and GUA, which received desalination plant effluents, both showed greater rates of salinity increase (2.2 ppt/day and 2.1 ppt/day, respectively) and somewhat greater water loss (50 m^3/day-ha and 44 m^3/day-ha, respectively) than did BAN. Water input to BEL could not be estimated, but in GUA the volume of desalination effluents was reported to be 105 m^3/day (Lynford Cooper, pers. comm. 1997). Water loss from GUA must, therefore, have totalled 190 m^3/day (105 m^3/day + (1.9 ha x 44 m^3/day-ha)), or 100 m^3/day-ha. It is unlikely that evaporation alone can explain this quantity of water loss; hence, through-ground drainage presumably contributed to water loss at GUA.

Through-ground drainage could have been facilitated in GUA by an artificially high water level maintained by the input of desalination plant effluents. This hypothesis may also explain why GUA did not reach the high salinities of BEL and SAL, since drainage, unlike evaporation, removes salts as well as water. The sediments at GUA were sandy and porous, while those at BEL, SAL and BAN (Table 4.1) were composed of organic mud and often covered by thick layers of microbial mat, which have been shown to seal the bottoms of hypersaline water bodies (Borowitzka 1981; Burke 1995; Burke & Knott 1997; Davis 1978).

Table 5.2 Water loss and concentration of salts in ponds

a) Long-term water loss and salinity concentration during a drought (14 March, 1995, to 6 May, 1995)

Pond	Interval (1995)	Days	Salinity (ppt) initial - final	Change in Depth (cm/day)	Change in Salinity (ppt/day)	Evaporation (m^3/d-ha)
BAN	26 Mar - 26 Apr	31	160 - 200	-0.32	1.4	32
BEL	19 Mar - 26 Apr	38	160 - 350	-0.50	2.2	50[a]
GUA	18 Mar -14 Apr	27	79 - 140	-0.44	2.1	44[a]
SAL	5 Mar - 14 May	70	270 - 500	-0.13	3.2	13[ab]

[a]BEL, GUA and SAL received low-volume seawater input (see Sect. 4.2 (a.*i* , a.*iv*))
[b]Sampling interval was not completely within period of drought

b) Short-term water loss

Pond	Date (2000)	Time Interval	Salinity (ppt)	Weather	Depth Change (cm)	Evaporation (m^3/d-ha)
BAN	17-18 Apr	16:30- 10:00	-	clear	-0.33	45
	20-Apr	9:30- 18:30	-	prt cloudy	-0.12	32
	13-14 Aug	21:30- 7:20	80	night	0	0
JOS	18-Apr	9:00- 16:50	-	clear	-0.5	150
	26-Jul	13:30- 17:40	124-130	prt cloudy	-0.24	140
	26-Jul	17:40- 21:40	130	prt cloudy	-0.09	54
	26-27 Jul	21:40- 7:00	129	clear	0	0

5.2 (a.*iii*) Summary of hydrological and salinity variation among salt ponds

Temporal variation in salinity was controlled mainly by seasonal fluctuations in rainfall. Spatial variation in salinity, however, was controlled by a pond's specific hydrological characteristics, which also determined its period of inundation. This relationship between hydrological (Chapter 4) and salinity variation is summarised as follows.

- Non-permanent ponds with no visible sea connection: Inundation in these ponds was entirely controlled by rainfall and evaporation, as demonstrated by the inability of extreme high tides to inundate these ponds during the dry season. Nevertheless, the bottoms of about ½ of these ponds must have been very near sea level because tidal changes in sea level caused fluctuations in pond level, presumably by building and slackening pressure in the ground water. Other non-permanent ponds were shallower and did not experience such tidal fluctuations. Non-permanent ponds without sea connections experienced low salinities near that of seawater and high salinities up to 130 ppt (mean 52 – 84 ppt).
- Non-permanent ponds with periodic direct sea connection: Water levels in these ponds were controlled by tidal fluctuations when sea level was sufficiently high to maintain communication between the pond and the sea. When sea level was low, this communication was broken, and then water levels were controlled by rainfall and evaporation cycles. Unlike other non-permanent ponds, ponds with periodic direct sea connection could be filled from dryness by sea overwash during seasonally high sea levels. The magnitude (but not the timing) of salinity fluctuations was similar to those in other non-permanent ponds.
- Permanent ponds with no visible sea connection: Two ponds with dissimilar hydrologies fitted this description. Water level in one (BAN) was influenced by rainfall and evaporation but not by tidal fluctuations. The other (SIN) was greatly influenced by sea level changes. Salinity in BAN was generally high (mean 100 ppt) and fluctuated enormously (46 to 220 ppt) during the course of this study. Salinity in SIN, in contrast, was usually just above seawater (mean 44 ppt) and remained low (35 - 51 ppt) even during times when dry weather occurred in conjunction with low sea level (February – April).

  SIN's unique hydrology, characterized by high-amplitude tidal fluctuations, permanent inundation and near-seawater salinity, suggests that this pond maintained underground connection with the sea, probably through its coral berm. Such hydrology is similar to that of the anchialine ponds of Bermuda, which maintain sea connection through underground caves (Por 1985; Thomas *et al.*, 1991).

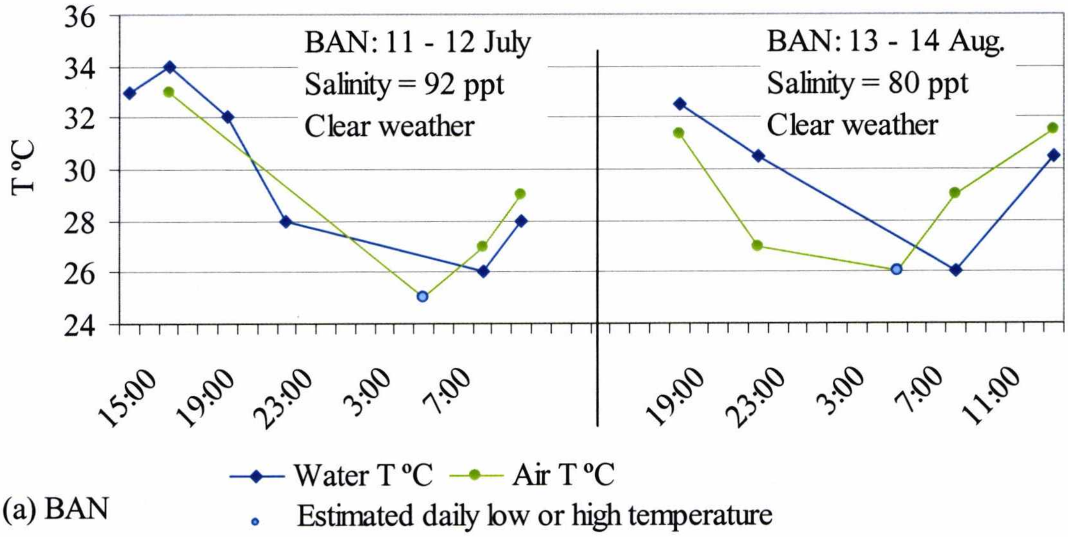
- Permanent ponds with seawater seeps: Inundation in ponds with seawater seeps was maintained via constant inward seepage of seawater. Water level was determined primarily by rainfall and evaporation, though small daily fluctuations in water level corresponded with tidal cycles. Ponds with seawater seeps experienced the highest salinities of all ponds (mean annual salinities ranged from 150 to 320 ppt). Calcite, gypsum and sodium chloride were deposited by precipitation in these ponds during the dry season.
- Permanent ponds with direct sea connection: Water level in ponds with permanent direct sea connection was controlled by sea level fluctuations and by rainfall and evaporation. Salinity was variable but generally high (mean annual salinities ranged from 80 to 100 ppt). Rainfall and evaporation appeared to be far more important in forcing salinity fluctuations than was seawater flushing, a pattern observed in hypersaline lagoons elsewhere (Kjerfve *et al.* 1996; Kristensen & Hulsher-Emeis 1972)

5.2 (b) Water temperature

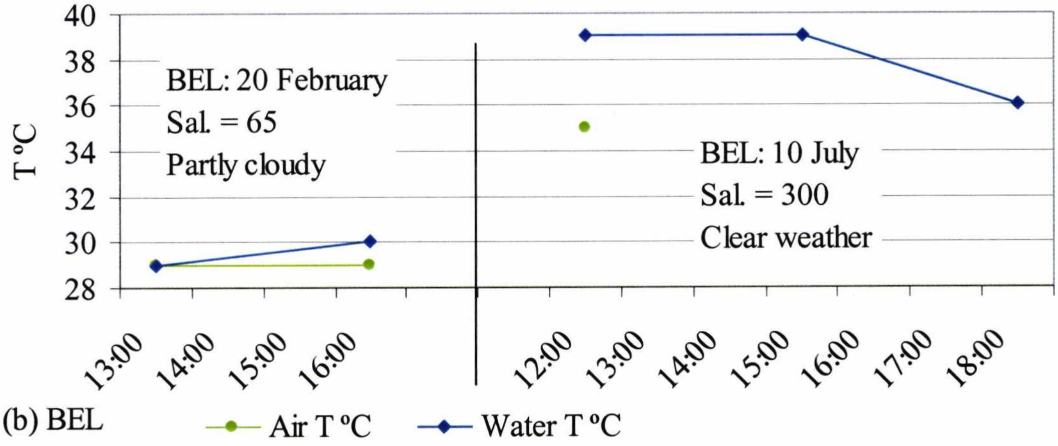
Mean daytime water temperatures (for ponds with more than 3 samples) ranged from 30 ± 7.3°C in JOS to 38 ± 3.6°C in SAL (Table 5.1). Temperatures of up to 45°C were recorded in SAL under highly saline conditions (> 350 ppt). Maximum temperatures recorded in other ponds did not exceed 41°C. Temperatures greater than 35°C are known to limit eukaryotic organisms (Gunter 1967; Kantrud 1991; Kristensen & Hulsher-Emeis 1972; Larsen 1980; Robertson & Phillips 1995), and limiting temperatures occurred occasionally in all ponds. Record low temperatures between 16° and 18°C were recorded early in the morning in several ponds during October 1998 (see Appendix B), but otherwise all temperatures recorded between 1995 and 2000 were greater than 26°C.

Figure 5.4 illustrates daily temperature fluctuations in several salt ponds. Water temperatures on clear, sunny days were regularly 2 to 4°C warmer than air temperature by mid-afternoon (see Figure 5.4(b, d – f)). Figure 5.4(f) shows that even in a low-salinity pond (JOS at 33 ppt) water temperature can be elevated 4°C above ambient air temperature at mid-day with clear weather conditions. Water temperatures dropped after sunset, and by early morning they were usually at or below ambient air temperature (Figure 5.4(a, c – f)). These results are consistent with the expected properties of hypersaline waters (see Section 1.4 (c)).

The super-heating of pond water was caused by the high specific heat of water. Ponds with greater salinity were expected to become warmer than less saline ponds, but the observed effect of salinity on super-heating in ponds was variable because of such factors as cloudiness and orientation of a pond relative to the sun. Frequent monitoring within a single pond under varying salinity conditions but similar weather conditions should show a regular positive effect of increasing salinity on superheating.

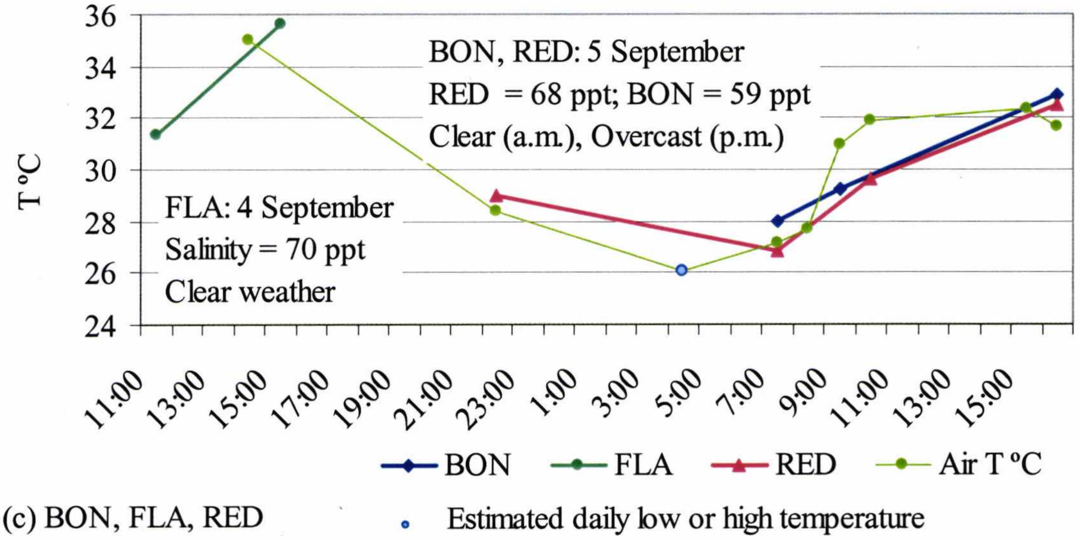


(a) BAN

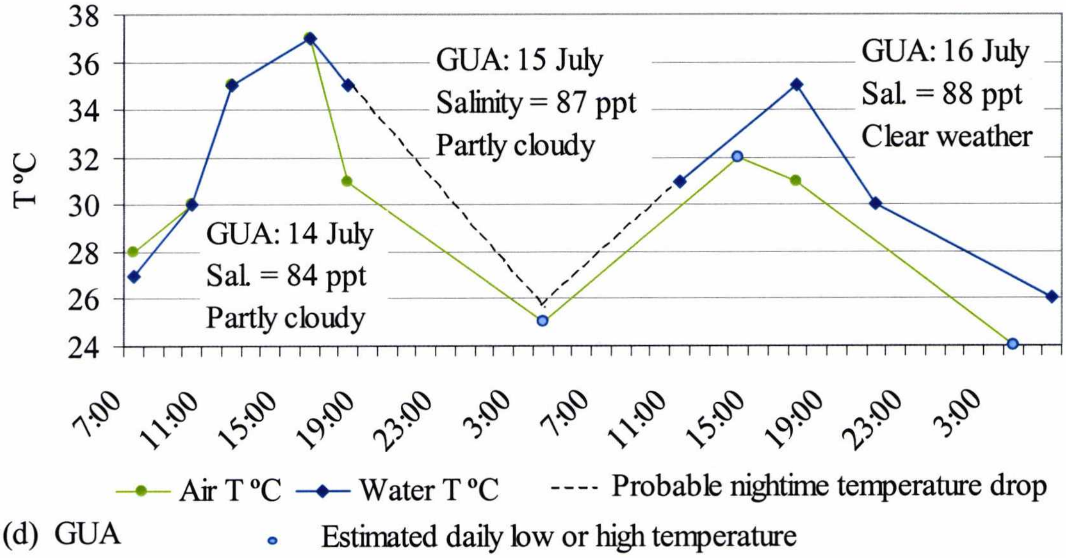


(b) BEL

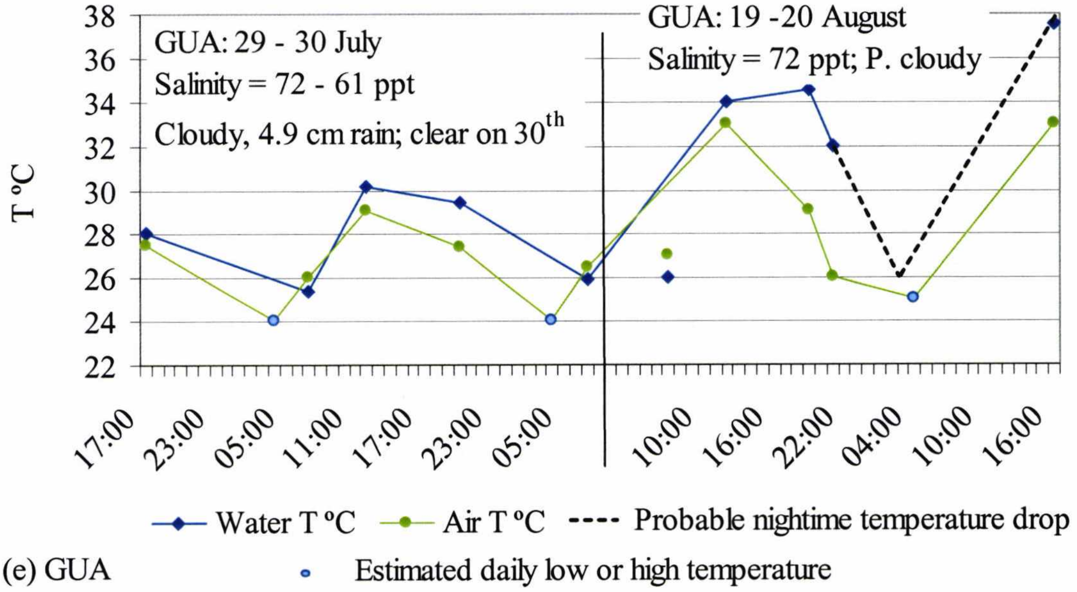
Figure 5.4 Daily temperature fluctuations in salt ponds (2000)



(c) BON, FLA, RED



(d) GUA



(e) GUA

Figure 5.4 (continued) Daily temperature fluctuations in salt ponds (2000)

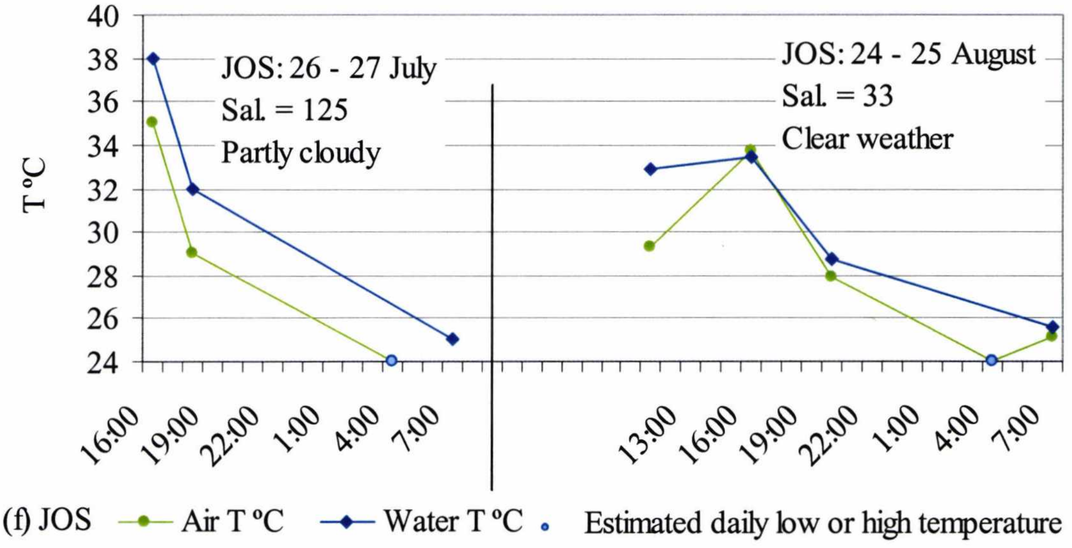


Figure 5.4 (continued) Daily temperature fluctuations in salt ponds (2000)

5.2 (c) Stratification

Figure 5.5 shows temperature stratification during the day on 14 July, 2000, in GUA. Surface water was warmer than either bottom water or air at 9:50 a.m. By mid-day, however, bottom water exceeded surface temperature by 2.2°C. Surface water temperature, presumably cooled by evaporation, remained below air temperature through mid-afternoon, while bottom water became superheated (1°C above air temperature). Pond water cooled more slowly than the air in the evening. Nighttime measurements were not taken, but temperature stratification caused by solar energy during the day should disappear as a result of mixing and heat conduction at night. Further sampling is required to determine how quickly stratification disappears in the absence of sunlight and whether some ponds (i.e. deeper ones) maintain temperature stratification over longer periods.

Salinity stratification occurred only after rainfall. After 6.5 cm of rain (on 28 and 29 July, 2000), surface water in GUA was 24 ppt less saline than bottom water (Figure 5.6). Surface and bottom salinity gradually approached equilibrium at 57 ppt (18 ppt lower than the pre-rain salinity) over a period of 48 hours. This pattern was repeated on a smaller scale after a rainfall of 0.18 cm on 19 August, 2000. This rainfall diluted surface water to 6 ppt less than bottom water (73 ppt), and equilibrium (71 ppt) was achieved after 9 hours. These observations indicate that salinity stratification caused by rainfall is short-lived and that pond waters were generally well mixed.

Small-scale salinity stratification may result from surface evaporation during the day, but measurement techniques used here were not sensitive enough to detect salinity differences of less than 1 ppt.

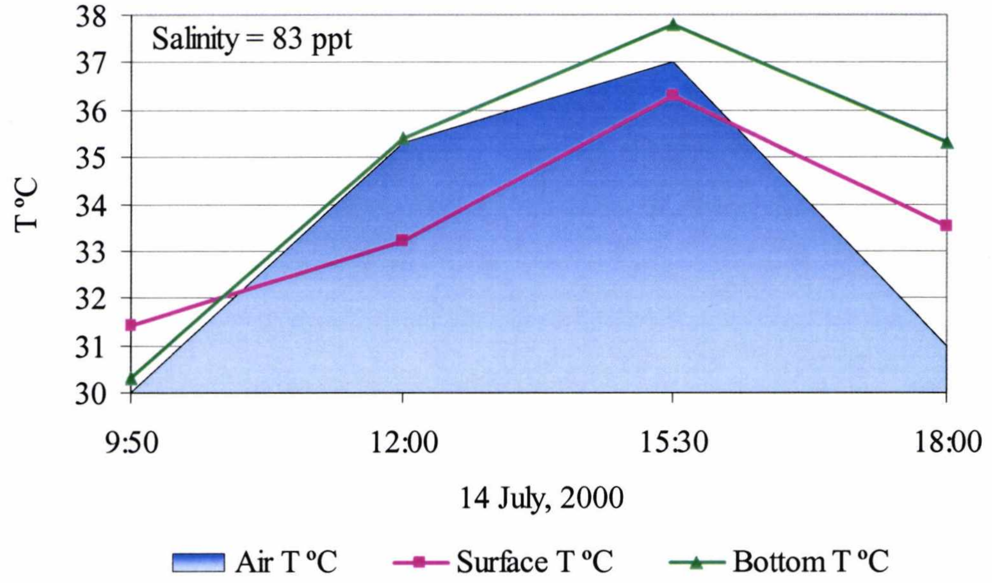


Figure 5.5 Temperature stratification in GUA

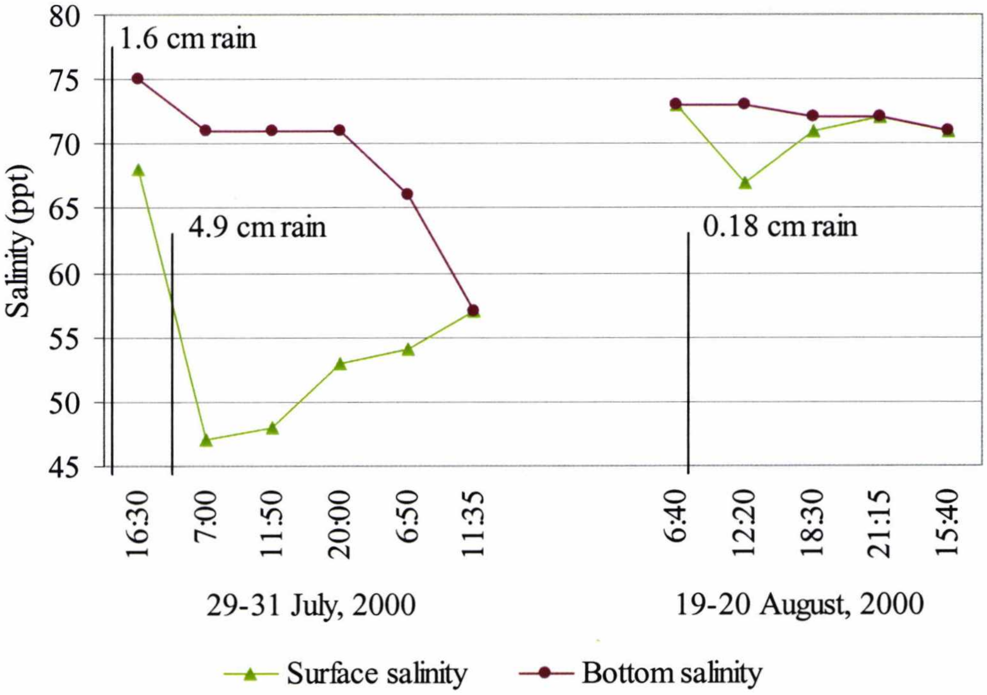
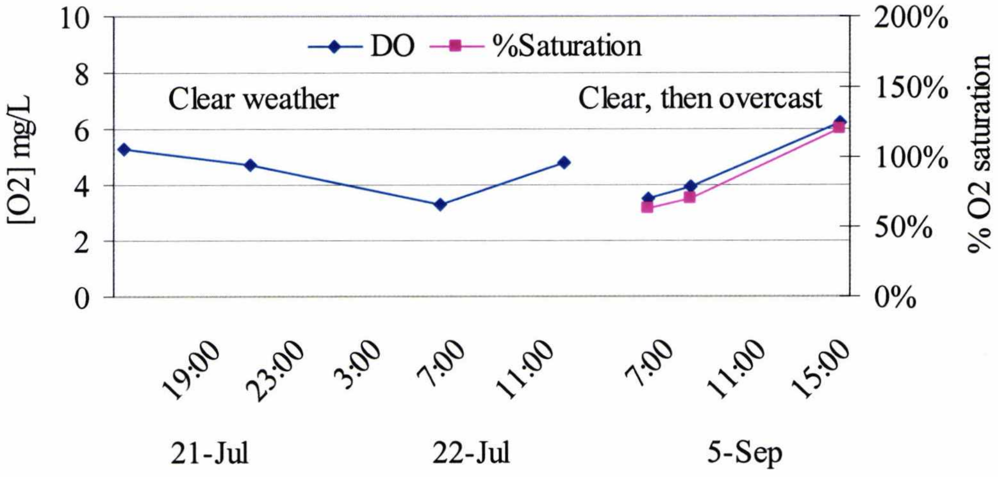


Figure 5.6 Salinity stratification in GUA

5.2 (d) Dissolved oxygen

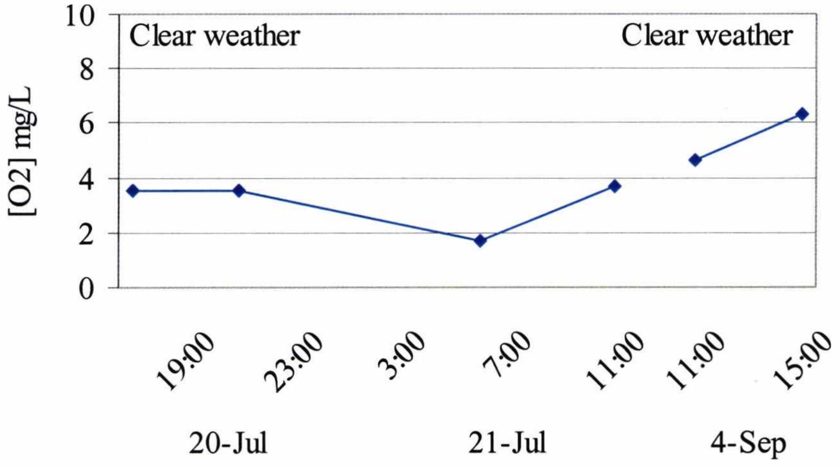
Mean concentrations of dissolved oxygen (DO) were lowest in high salinity ponds, in accordance with expectation (Table 5.1). Mean DO concentrations in high salinity ponds BEL and RED (2.3 ± 2.4 and 2.3 ± 2.3 mg/L) for example, were 4.7 mg/L and 6.8 mg/L lower than mean DO concentrations in lower salinity ponds GUA (7.0 ± 2.9 mg/L) and JOS (9.1 ± 4.7 mg/L), respectively. DO was not detectable at salinities greater than 270 ppt. DO concentrations in ponds at low salinities (< 45 ppt), on the other hand, regularly exceeded 10 mg/L (Appendix B).

Diurnal fluctuations in DO concentrations are shown in Figure 5.7. Diurnal variation was smaller in the Anegada ponds, BON (2.7 mg/L, Figure 5.7(a)), FLA (2 mg/L, Figure 5.7(b)) and RED (3.5 mg/L, Figure 5.7(g)) than in GUA (8 mg/L, Figure 5.7(c-e)) and JOS (7.5 mg/L, Figure 5.7(f)). Both GUA and JOS reached DO saturation levels of 150% or greater by mid-afternoon, reflecting a substantial contribution of DO by producers. At night, depletion of oxygen by respiration caused DO levels to fall below 50% saturation in GUA and JOS.

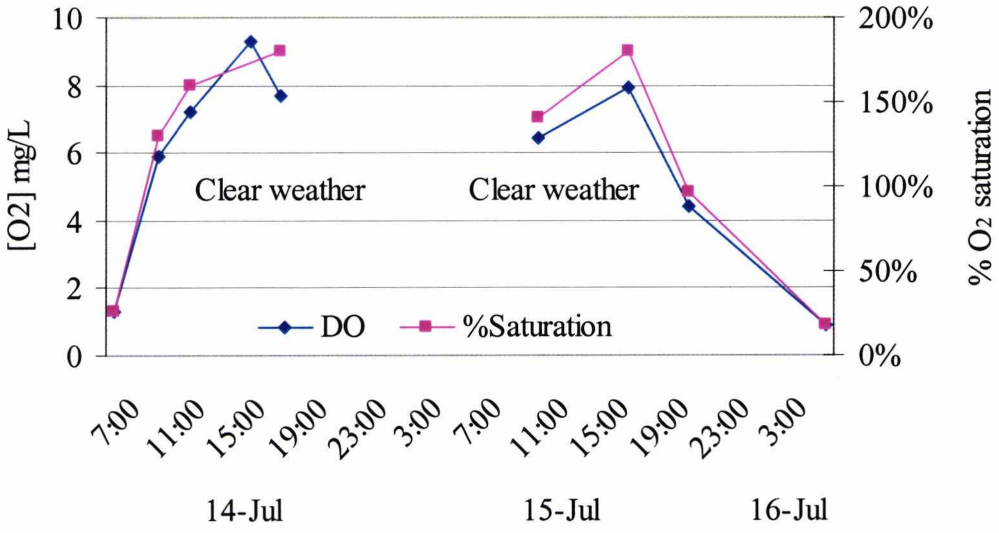


a) BON Dissolved Oxygen: 21 - 22 July and 5 September, 2000

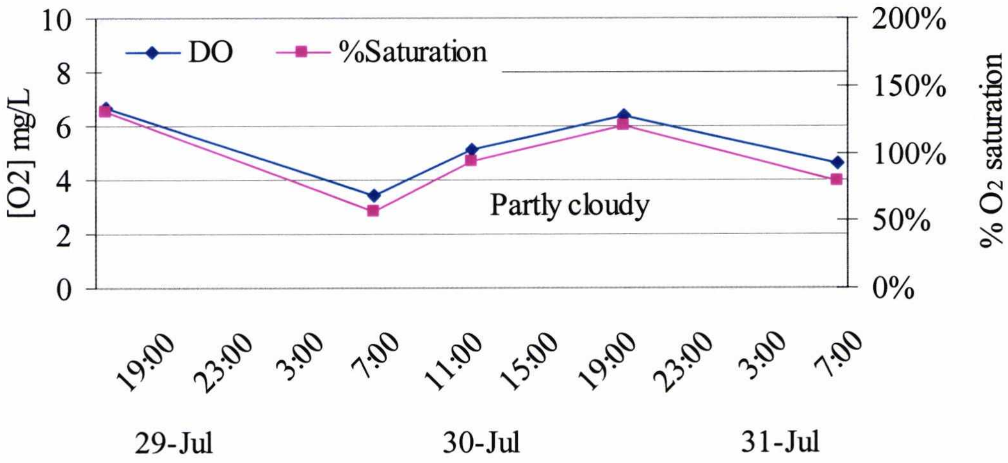
Figure 5.7 Diurnal fluctuations in dissolved oxygen concentration



b) FLA Dissolved Oxygen: 20 - 21 July and 4 September, 2000

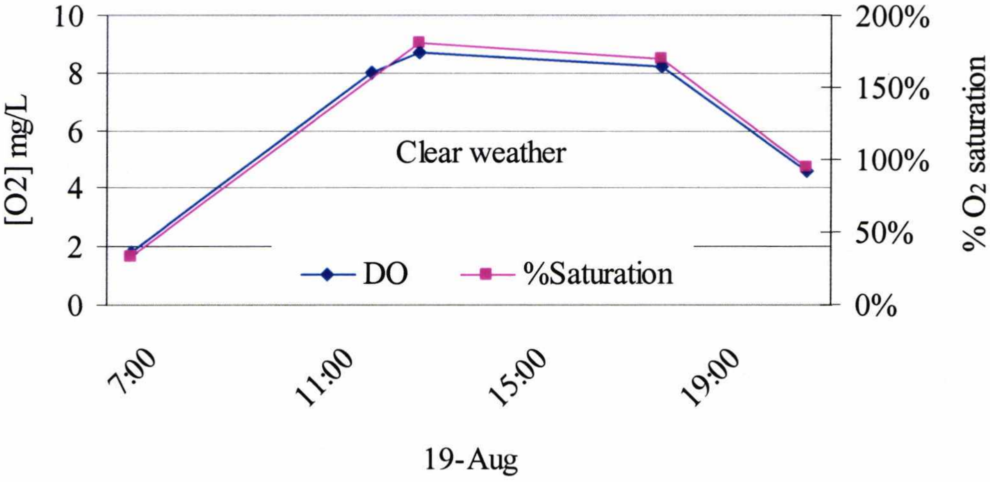


c) GUA Dissolved Oxygen: 14 - 16 July, 2000

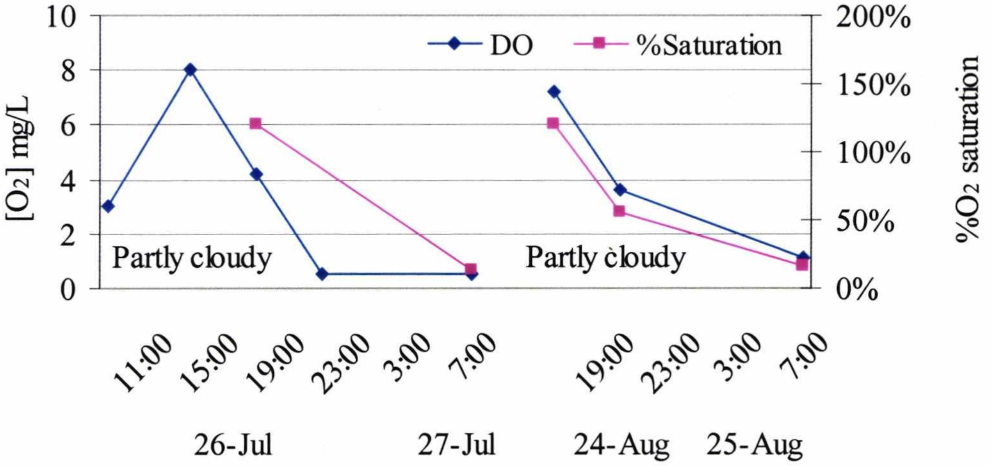


d) GUA Dissolved Oxygen: 29 - 31 July, 2000

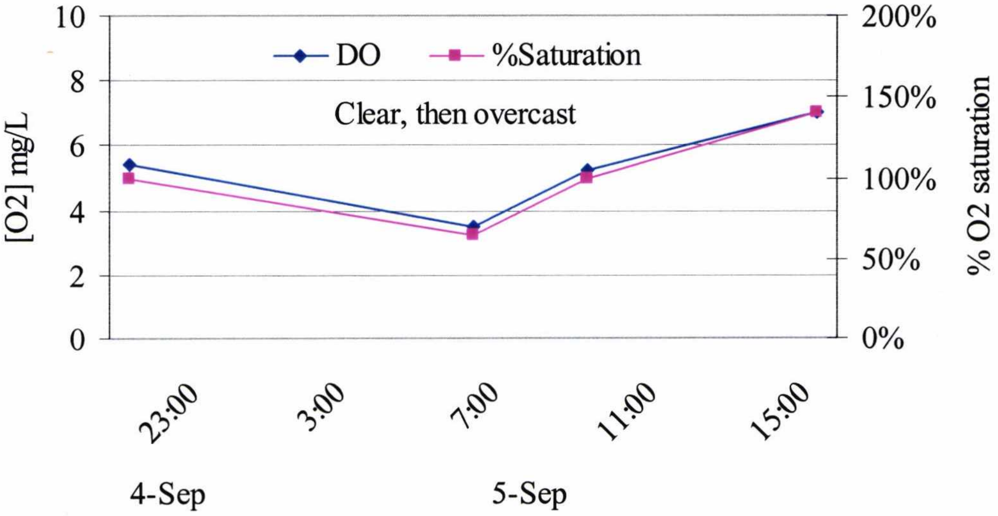
Figure 5.7 (continued) Diurnal fluctuations in dissolved oxygen concentration



e) GUA Dissolved Oxygen: 19 August, 2000



f) JOS Dissolved Oxygen: 26 - 27 July and 24 - 25 August, 2000



g) RED Dissolved Oxygen: 4 - 5 September, 2000

Figure 5.7 (continued) Diurnal fluctuations in dissolved oxygen concentration

The Anegada ponds showed smaller effects of photosynthesis and respiration on DO, which remained below 150% during the day but did not fall below 60% at night. Dominance of benthic microbial communities (BMCs) may be responsible for the lower DO fluctuations observed in the Anegada ponds because BMCs have less surface area in contact with the water column than other types of producers, such as *Ruppia* grass and phytoplankton that occurred in JOS and GUA (Figure 6.2). Photosynthesis in BMCs is restricted to the upper 5 mm of the mat (Des Marais 1995; Pinckney & Paerl 1997), only the surface of which contacts the water column. Furthermore, some of the oxygen produced by BMCs is consumed within the benthic mats rather than being exported to the water column (Burke 1995; Burke & Knott 1997; Canfield & Des Marais 1994; Des Marais 1995).

GUA did not have *Ruppia*, BMC or a visible phytoplankton bloom during any of the sampling periods shown in Figure 5.7(c - e). Nevertheless, photosynthesis, presumably from undetected planktonic and/or benthic producers, caused supersaturation greater than 150% on 3 out of 5 sampling dates, while DO levels dropped below 50% at night. Cloudy weather on 29 – 30 July, 2000, resulted in lower levels of daytime supersaturation in GUA (Figure 5.7(d)).

A visible green phytoplankton bloom in JOS, present during both sampling periods shown in Figure 5.7 (f), greatly increased DO concentrations during daylight. Percent saturation at mid-day on 26 July could not be calculated due to high water temperature (see Section 3.3 (d)), but at 8 mg/L, DO probably exceeded 150% saturation. Effects of the phytoplankton bloom were also evident at night, when DO saturation dropped below 20% (Figure 5.7 (f)).

All types of producer communities caused supersaturation of pond waters during mid-day and oxygen depletion at night, but the examples presented here show a difference in the magnitude of influence on DO concentrations of a water-column dominated producer community versus a benthic producer community. Quantification of this difference by future studies is justified by the biological importance of dissolved oxygen in hypersaline communities.

5.2 (e) pH

Mean pH ranged from 8.0 to 8.4 in all ponds except BEL, in which the mean of 3 samples was 7.3, and LON, in which the mean of 8 samples was 8.8 (Table 5.1). The mean pH reported for LON is artificially high because 5 samples (all with values of 9.0) out of the 8 total samples were taken within one month of Hurricane Georges. pH in LON was 8.5 at other times, and this value is more likely to reflect the true mean in LON. Low pH (less than 8.0 in seawater) was associated with salinities high enough to cause precipitation of major ions. Several authors have reported decreasing pH with increasing salinity, but the lowest pH predicted for coastal hypersaline water bodies is 7.8 (Carpelan 1957; Copeland 1967) and the lowest pH reported is 7.2 (Britton & Johnson 1987; Goodwin *et al.* 1984; Kristensen 1964; Pinckney & Paerl 1997; Victor *et al.* 1997). This study recorded pH values below 7.2 three times: in JOS immediately after a heavy rainfall (pH = 6.5; salinity = 12 ppt; 23 Oct., 1998), in SAL at 360 ppt salinity (pH=7.1; 8 July, 2000), and in BEL at 300 ppt salinity (pH=6.8; 10 July, 2000, see Appendix B).

pH values greater than 9.0, limiting to most photosynthetic organisms because of the depressed solubility of CO_2 (Carpelan 1957; Copeland 1967), were never observed. pH values as high as 9.0 were observed only after Hurricane Georges (September, 1998) in JOS and LON. All other pH measurements in ponds were 8.8 or less.

5.2 (f) Turbidity

Pond water was usually clear, with mean turbidities less than 60 FAU (see Table 5.1 and Appendix B). Turbidity greater than 100 FAU in combination with a green or red colour was indicative of phytoplankton blooms. Blooms of green phytoplankton in JOS were coincident with turbidities of 130 – 230 FAU (26 July, 2000, and 24 August, 2000). Green phytoplankton blooms were observed visually, but without corresponding turbidity measurements, at other times in all of the lower-salinity ponds, including GUA, JOS and WB. A turbidity of 290 FAU and brick-red colour was recorded in RED on 16 February, 2000. Microscopic examination revealed that the water column was filled with a flocculent gelatinous cyanobacteria.

Greyish-coloured water with elevated turbidity was observed 3 times in GUA (20 September, 1998, 74 FAU, 1 July, 2000, 84 FAU, and 14 July, 2000, 110 FAU) and once in FLA (16 Feb, 2000, 76 FAU). Corresponding salinities were between 77 and 83 ppt, just above the concentration at which calcite ($CaCO_3$) begins to precipitate out of seawater. The observed greyish colour and elevated turbidity probably resulted from calcite precipitation events, though the effects of other factors, such as wind and runoff, were not evaluated. Elevated turbidity resulting from gypsum ($CaSO_4$-$2H_2O$) precipitation has been reported in hypersaline ponds of Curacao (Kristensen & Hulsher-Emeis 1972), but data taken in this study did not include turbidity readings near the precipitation point of gypsum (175 ppt).

5.2 (g) Nutrients (N and P)

Mean nutrient concentrations are shown in Table 5.3 and all records are listed in Appendix C. Nitrate concentrations averaged between 1.1 and 1.6 NO_3^--N mg/L in BAN, LON, JOS, SIN and GUA. The Anegada ponds exhibited somewhat higher mean nitrate concentrations, ranging from 2.1 ± 1.6 mg/L(BON) to 3.8 ± 2.0 NO_3^--N mg/L (FLA). Greatest nitrate concentrations, on average, were found in BEL, with 4.9 ± 1.1 NO_3^--N mg/L, though the maximum recorded concentration (6.7 NO_3^--N mg/L) occurred in FLA (see Appendix C). Nitrate concentrations in ponds were between 3 and 14 times the concentrations found in normal open coastal marine waters in the BVI (0.34 ± 0.11 mg/L NO_3^--N between May, 2000, and January, 2001, N=18).

Mean nitrite concentrations ranged from 1 to 10 μg/L NO_2^--N, and concentrations varied within ponds as much as between ponds (Table 5.3 and Appendix C). Nitrites, on average (4 ± 5 μg/L NO_2^--N, across all ponds), were nearly twice as concentrated and many times more variable than they were in BVI coastal waters (2 ± 1 μg/L NO_2^--N between May, 2000, and January, 2001, N=6).

Mean ammonia concentrations in salt ponds ranged from 0.18 ± 0.05 mg/L NH_3-N in BON to 0.84 ± 0.6 mg/L NH_3-N in BEL (Table 5.3). Ammonia concentrations in BEL, FLA, PTP, RED and SAL were higher than in BON and GUA, and intermediate levels were found in BAN, JOS and WB. Ammonia concentrations in all ponds were elevated 2 to 11 times above open coastal waters (0.08 ± 0.06 mg/L NH_3-N, May, 2000, to January, 2001, N=18).

Phosphate concentrations in ponds were normally less than 0.15 PO_4^{3-} mg/L, though concentrations up to 0.38 PO_4^{3-} mg/L occurred (Appendix C). Occasionally phosphate concentrations fell below detectable limits (<0.01 mg/L). Nevertheless, the concentration of phosphates in salt ponds was often far greater than that found in the BVI's open coastal marine waters (<0.01 mg/L PO_4^{3-}, May, 2000, to January, 2001, N=18).

Table 5.3 Summary of nutrient concentrations in salt ponds. Values are shown as $\overline{x} \pm \sigma$ (N).

Pond	NO_3^--N (mg/L)	NO_2^--N (µg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
BAN	1.3 ± 0.64 (13)	1 ± 2 (8)	0.39 ± 0.20 (7)	0.06 ± 0.11 (12)
BEL	4.9 ± 1.1 (3)	10 ± 6 (6)	0.84 ± 0.60 (6)	0.16 ± 0.12 (3)
BON	2.1 ± 1.6 (5)	2 ± 1 (5)	0.18 ± 0.05 (3)	0.06 (1)
FLA	3.8 ± 2.0 (4)	5 ± 5 (6)	0.51 ± 0.45 (4)	0.12 ± 0.01 (2)
Gr. Harbour	0.40 (1)			0.01 (1)
Great Thatch	0.40 (1)			0.02 (1)
GUA	1.3 ± 0.84 (11)	2 ± 2 (6)	0.19 ± 0.07 (5)	0.02 ± 0.02 (7)
JOS	1.3 ± 1.4 (10)	8 ± 5 (4)	0.34 ± 0.18 (5)	0.14 ± 0.14 (9)
LON	1.1 ± 0.35 (8)			0.02 ± 0.02 (8)
Manhead	2.6 (1)	0 (1)		
PTP	2.3 (1)	5 ± 8 (3)	0.60 ± 0.29 (2)	
RED	2.3 (1)	7 ± 8 (3)	0.58 ± 0.72 (2)	
SAL		0 (1)	1.3 (1)	0 (1)
SIN	1.6 ± 0.31 (2)	3 ± 1 (2)	0.17 (1)	0.03 ± 0.02 (2)
WB		2 ± 3 (2)	0.39 ± 0.25 (3)	

This chapter illustrated the control of salinity by hydrological factors, and it described the spatially and temporally variable chemical characteristics of salt ponds. It focussed on chemical parameters that are important to biological communities, which are the subject of the next chapter.

Chapter 6: Community Structure and Dynamics

6.1 Introduction

Aquatic communities inhabiting hypersaline waters are known to have reduced faunas (see Section 1.4 (f)). Salinity and covarying physical and chemical factors, such as oxygen solubility, temperature and the presence of water, ultimately restrict the composition of hypersaline communities (Williams & Kokkin 1988). The taxa that are able to withstand hypersaline conditions generally have wide distributions (Bayly 1972; Hammer 1986), suggesting that environmental factors are more likely to limit their distribution than are geographic factors.

Halotolerant species occur within particular salinity ranges (Bayly 1972; Britton & Johnson 1987; Colburn 1988; De Decker & Geddes 1980; Garcia & Niell 1993; Garcia *et al.* 1997; Hammer 1986; Lonzarich & Smith 1997; Williams 1998), but salinity limits may vary among locations due to differences in other biologically significant factors such as ionic composition (Armengol & Miracle 1999), sediment composition (Guerrero *et al.* 1994; Herbst 1990; Waterman *et al.* 1999), and the presence of certain vegetation types (Athersuch *et al.* 1999; Verschuren *et al.* 2000). In addition to spatial variations, several authors (e.g. Beadle 1943, Borowitzka 1981, Britton & Johnson 1987, Garcia *et al.* 1997 and LaBarbera & Kilham 1974) have described temporal changes in species composition in water bodies with fluctuating salinities.

Herbst (1988) proposed that salinity forcing only operates near the limits of a species' physiological tolerance and that the distribution of halotolerant species is otherwise determined by biotic factors. However, few examples of biotic controls in hypersaline communities currently exist (Williams 1998).

The purpose of this chapter is firstly to describe the composition of salt pond communities in the BVI and secondly to consider the question of whether salinity and/or biotic controls predominate in determining community dynamics in these hypersaline ecosystems.

6.2 Results and discussion

6.2 (a) The salt pond community

All organisms that were recorded within salt ponds and on their shores between 1991 and 2001, with the exception of birds, are listed in Table 6.1.

Table 6.1 Species list, BVI salt ponds

Group Name	Occurrence in salt ponds
Pisces	
Elops sp. (ten pounder)	uncommon
Mugil sp. (mullet)	uncommon
Ulaema lefroyi Goode (mottled mojarra)	uncommon
Arthropoda	
Decapoda	
Uca burgersi Holthuis (fiddler crab)	common
Callinectes sapidus Rathbun (blue crab)	uncommon
Cardisoma guanhumi Latreille (great land crab)	uncommon
Branchiopoda	
Artemia franciscana Kellogg	common
Copepoda	
Cyclopoida:	
Apocyclops panamensis Marsh	common
Harpactacoida:	
Cletocamptus albuquerquensis Herrick	common
Cletocamptus deitersi Richard	common
Metis	rare
Nitocra	rare
Ostracoda	
Perissocytheridae cribrosa Klie	uncommon
Thalassocypria inopinata Klie	uncommon
Insecta, aquatic	
Berosus metalliceps Sharp (hydrophilid beetle)	uncommon
Aedes taeniorhynchus Wiedemann (salt marsh mosquito)	rare
Dasyhelea sp. (biting midge)	common
Ephydra gracilis Packard (brine fly)	uncommon
Eretes sticticus Linne (water beetle)	uncommon
Trichocorixa reticulata Guérin Méněville (corixid)	common

Table 6.1 (continued) Species list, BVI salt ponds

Group Name	Occurrence in salt ponds
Insecta, shore	
Cicindela boops Dejean (tiger beetle)	---
Cicindela trifasciata Fabricius (tiger beetle)	---
Megacephala sobrina Dejean (tiger beetle)	---
Pentacora signoreti Guérin Ménéville (shore bug)	---
Molluscs	
Anomalocardia brasiliana Conrad (bivalve)	Anegada
Batillaria minima Gmelin (gastropod)	Anegada
Cerithidea costata da Costa (gastropod)	Anegada
Cerithium lutosum Menke (gastropod)	Anegada
Pyrgophorus sp. (gastropod)	uncommon
Truncatella sp. (gastropod, shoreline)	Anegada
Rotifera	uncommon
Protists	
Ciliophora	common
Turbellaria (flatworms)	---
Chlorophyta	
Dunaliella sp.	rare, Aneg.
Macroalgae	
Cladophora	---
Rhizoclonium	common
Microbial mats	
Cyanobacteria	
Aphanothece pallida (Kützing) Rabenhorst	common
Chroococus minutus (Kützing) Nägeli	common
Coccochloris stagnina Drouet *et* Daily	common
Gomphosphaeria salina Komarek *et* Hindak	BON
Johannesbaptistia pellucida Taylor *et* Drouet	rare
Oscillatoria spp.	common
Microcoleus cthonoplastes Thuret	common
Phormidium spp.	common
Schizothrix mexicana Gomont	common
Spirulina subsalsa Oersted	common
Symploca cf. laete-viridis Gomont	uncommon
Sulphur bacteria	common
Chromophyta	common

Table 6.1 (continued) Species list, BVI salt ponds.

Group Name	Occurrence in salt ponds
Microbial mats (continued)	
Diatoms	
Navicula	common
Gomphipora	common
Surirella	common
Nitzschia	common
Dinoflagellates	uncommon
Foraminiferans	common
Nematodes	common
Plants	
Aquatic Grass	
Ruppia maritima Linne (wigeongrass)	uncommon
Shore plants	
Batis maritima Linne (saltwort)	common
Borrichia arborescens Linne (sea ox-eye)	Anegada
Sporobolus virginicus (L) Kunth (seashore rush grass)	common
Heliotropium curassavicum Linne (seaside heliotrope)	uncommon (common at WB)
Salicornia bigelovii Torr (glasswort)	Anegada
Sesuvium portulacastrum Linne (sea purslane)	common
Strumpfia maritima Jacquin (strumpfia)	Anegada
Mangrove trees	
Avicennia germinans Linne (black mangrove)	common
Conocarpus erectus Linne (buttonwood)	common
Laguncularia racemosa Linne (white mangrove)	common
Rhizophora mangle Linne (red mangrove)	common

6.2 (a.*i*) The shore community

Great land crabs, *Cardisoma guanhumi*, were common in the surrounding mangrove forests, but fiddler crabs, *Uca burgersi*, dominated the shore fauna at most salt ponds. These fiddler crabs lived in burrows along pond shores. Specimens from JOS collected in 1995 were the largest *U. burgersi* on record (Zimmerman, pers. comm. 1998). The larvae of *U. burgersi* were captured in plankton samples from ponds. Members of the genus *Uca* are known to lay eggs in estuarine waters (Dittel & Epifanio 1990), but the presence of *Uca* larvae in enclosed saline ponds has not been previously reported.

Insects, notably tiger beetles *Megacephala sobrina, Cicindela trifasciata*, and *Cicindela boops* and shore bugs, *Pentacora signoreti*, frequented pond shores. *Cicindela boops* is described by Ivie (1983) as the rarest cicindelid in the Virgin Islands. He has also suggested that *C. boops* may be a salt-pond specialist (Ivie, pers. comm. 2001).

Plant communities fringing the shores of BVI salt ponds were typical of Caribbean basin mangrove ecosystems (Carlton 1975; Lewis 1990; Nellis 1994; Rooth 1965, 1967). Common shore vegetation included rush grass, *Sporobolus virginicus*, saltwort, *Batis maritima*, and seapurslane, *Sesuvium portulacastrum.* Seaside heliotrope, *Heliotropium curassavicum,* was common only at WB. Glasswort, *Salicornia bigelovii,* was common only around the salt ponds of Anegada. Sea ox-eye, *Borrichia arborescens*, and strumpfia, *Strumpfia maritima,* were also particularly abundant around the Anegada salt ponds. Mangrove forests grew around the edges of nearly all ponds (see Section 4.2 (d)).

6.2 (a.*ii*) Aquatic biota

The most common of the aquatic macrofaunal species were brine shrimp (*Artemia franciscana*) fly larvae (*Ephydra gracilis* and *Dasyhelea* sp.) and water boatmen (*Trichocorixa reticulata*). *Artemia franciscana* is known from saline waters throughout the Americas, and it is abundant in Caribbean salterns (Kristensen & Hulsher-Emeis 1972; Nixon 1970; Persoone & Sorgeloos 1980). *Ephydra gracilis,* has been reported from Caribbean salterns (Kristensen & Hulsher-Emeis 1972; Walker 1962) and the genus is present on all continents except Australia (Herbst 1990). *Dasyhelea*, a midge, does not appear on species lists from inland salt lakes, coastal salt ponds, or salterns, though it is known to be euryhaline (John Epler, pers. comm. 1999). It was abundant in the sediments in BVI ponds, and it tolerated salinities over 100 ppt. *Trichocorixa reticulata* has a neotropical distribution (Balling & Resh 1984), and it has been previously reported from coastal hypersaline ponds in the Caribbean (Walker 1962).

Microfauna included copepods (*Apocyclops panamensis, Cletocamptus albuquerquensis* and *Cletocamptus deitersi*), rotifers, and ciliates. *Apocyclops panamensis* (a cyclopoid copepod) occurs throughout the tropical Americas (Por &

Reid 1990), and it is common in coastal salt ponds (Suarez-Moralez *et al.* 1999). *Cletocamptus albuquerquensis* has a circumtropical distribution while *C. deitersi* occurs throughout the Americas (Por & Reid 1990). This is the first study, however, to show both *C. albuquerquensis* and *C. deitersi* occurring in the same water body. Ciliates are typical members of saline lake faunas around the world (Garcia & Niell 1993; Simpson *et al.* 1998), and those most often captured in BVI ponds were large, planktonic and similar in appearance to *Fabrea salina* (as illustrated in Post *et al.* 1983), but this identification was not verified. Rotifers captured from BVI ponds were similar in appearance and habitat to the cosmopolitan genus *Brachionus,* though this identification was also not verified.

Ostracods have often been reported from hypersaline water bodies (Athersuch *et al.* 1989; Bayly 1993; Cole 1968; Garcia & Niell 1993; Lonzarich & Smith 1997), but the 2 species collected from BVI ponds, *Perissocytheridae cribrosa* and *Thallassocypria inopinata*, have not been previously described as components of hypersaline communities (see De Decker 1981 for the most recent review).

Mosquito larvae, *Aedes taeniorhynchus*, were rare in salt ponds. Another mosquito, *Culex bahamensis*, was found in small, low salinity pools within the mangrove forest adjacent to the ponds, but they were not found in salt ponds.

A diving beetle, *Berosus metalliceps,* and a water beetle, *Eretes sticticus,* were observed infrequently. These coleopterans are known from saline lakes throughout the world (Colburn 1988; Lahr *et al.* 1999; Timms 1998; Williams & Kokkinn 1988). Aquatic beetles were never caught in plankton tows, though they were observed swimming or clinging to rocks and they were captured in light traps during 2000 and 2001. Light traps also produced several infaunal organisms that were never recorded from plankton tows, including nematodes, small infaunal ciliates, and one turbellarian.

Marine taxa occurred only in ponds having direct sea connection (the Anegada pond and, intermittently, WB and LON), and they entered ponds only under low hypersaline conditions. They included fish (*Elops* sp., *Mugil* sp. and *Ulaema lefroyi*), harpacticoid copepods (*Metis* sp. and *Nitocra* sp.) and the estuarine crab *Callinectes sapidus*. *Elops* and *Mugil* have been reported from coastal saline ponds in the Americas and Europe (Britton & Johnson 1987; Gunter 1967; Kristensen 1971). *Metis* has been previously reported from coastal salt ponds and salterns in the Caribbean (Britton & Johnson 1987;

Suarez-Morales *et al.* 1999), and *Nitocra* has been reported from both inland and coastal saline waters in the Americas, Europe and Africa (Bayly 1972; Hammer 1986; Por & Reid 1990). Decapods do not inhabit inland saline waters (Williams 1985), but *Callinectes* has been reported from coastal salterns (Mustafa *et al.* 1999).

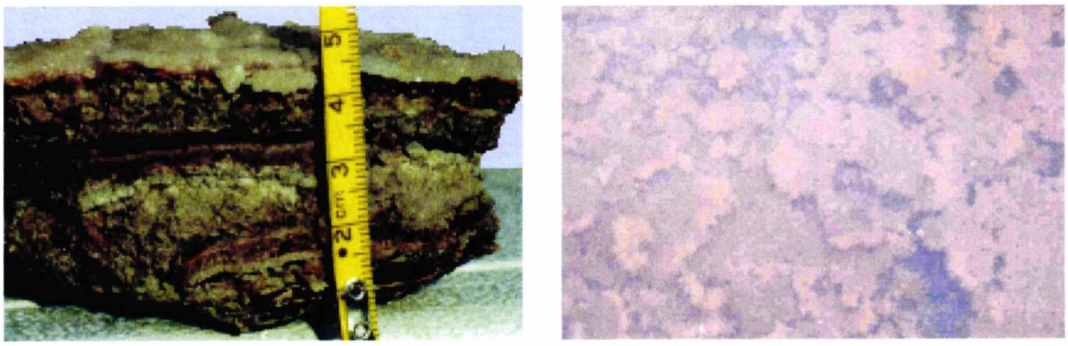
Molluscs were rarely found alive, probably because the benthos was not specifically sampled. However, one bivalve (*Anomalocardia brasiliana*) and 2 gastropods, (*Batillaria minima* and *Cerithium lutosum)* were so common at the Anegada ponds and particularly at RED and FLA that their dead shells formed a pavement along some parts of the shorelines. These gastropods have also been reported from salterns in Curacao (Kristensen & Hulsher-Emeis 1972) and the Bahamas (Hedgepeth 1959). Shells of 2 other gastropods (*Cerithidea costada* and *Truncatella* sp.), occurred less commonly at Anegada's ponds. *Truncatella* was found near the shoreline vegetation rather than in the ponds. These 5 species were not found on other islands. A much smaller snail, *Pyrgophorus* sp., was collected from GUA, LEE, and the Beef Island salt flats.

Planktonic chlorophytes occasionally became abundant enough to colour the water in some ponds (see Section 5.2 (f)), but organisms responsible were not specifically identified. The planktonic halophyte *Dunaliella* sp. was typically absent from BVI salt ponds, and its characteristic magenta-coloured blooms were encountered only 3 times, always on Anegada. The green macrophyte, *Rhizoclonium* sp., often in association with *Cladophora* sp., grew in tufts attached to sticks, rocks, or grass or it formed floating algal mats. Wigeongrass, *Ruppia maritima,* was common in some ponds during the rainy season. It formed vast underwater meadows rooted to the sediments but with leaves reaching the water surface. *R. maritima,* has a cosmopolitan distribution (Kantrud 1991), and it has been reported from salt ponds in the U.S. Virgin Islands (Norton *et al.* 1986), the Dominican Republic and St. Martin (Scott & Carbonell 1986). Both *Rhizoclonium* and *Ruppia* are frequent inhabitants of coastal ponds in North America (Carpelan 1957; Cornee *et al.* 1992; Des Marais 1995).

A variety of cyanobacteria, purple sulphur bacteria, diatoms, dinoflagellates, chromophytes, and foraminiferans formed benthic microbial communities (BMCs). BMCs occurred in several characteristic forms: as thin, 0.1 to 0.5 cm, green, firm-textured mats with little to no layering (Figure 6.1(a)); as thick, 1 – 4 cm, blue-black, layered and gelatinous mats with a thin brick-red surface layer, a subordinate thin green layer followed by a thick blue-black layer (Figure 6.1 (b – c); or as a loose, flocculent mass of orange-red cells (red floc, Figure 6.1(d)). Nematodes also inhabited these BMCs. The species composition and appearance of these BMCs were similar to those described from saline ponds around the world (Alcorlo *et al.* 2001; Borowitzka 1981; Des Marais 1995; Grey *et al.* 1990; Jorgensen 1989; Pinckney & Paerl 1997; Pinckney *et al.* 1995; Williams 1998). The surface layers were comprised mainly of cyanobacteria and diatoms, while bottom layers, specifically in blue-black BMCs, were dominated by purple sulphur bacteria. Species composition within these mats, however, was surprisingly variable among ponds (Jarecki *et al.* in review).

a) Green BMC, WB 2000

b) Blue-black BMC, BAN 1997



c) Blue-black BMC with calcite/gypsum crust, RED 2000

d) Red floc, FLA 2003

Figure 6.1 Images of benthic microbial mats from BVI salt ponds

6.2 (b) Distribution of common biota among ponds

6.2 (b.*i*) Fauna

Occurrence frequencies and the distribution of aquatic taxa are summarized in Figure 6.2. *Apocyclops, Cletocamptus, Trichocorixa* and Ciliophora were the most widespread groups, occurring in 80% or more of the ponds sampled. Among these, *Apocyclops* and *Trichocorixa* occurred most commonly; they were recorded in nearly

50% of all samples. *Cletocamptus* occurred in 39% and ciliates in 24% of all samples. Fly larvae overall had a somewhat lower representation among ponds. *Dasyhelea* was more widespread than *Ephydra*, occurring in 53% and 33% of ponds, respectively, but both species occurred with approximately the same frequency (*Dasyhelea* 19% and *Ephydra* 14%). *Artemia* occurred frequently (39%) but was restricted to 53% of the sampled ponds. Ostracods, *Uca* larvae, and rotifers all occurred in about half of the ponds sampled (53%, 47%, and 47% of ponds, respectively), but they were generally uncommon (12%, 11%, and 5% of samples, respectively). The scarcity of rotifers, in particular, was surprising because other studies have shown rotifers to be one of the most prevalent taxa in hypersaline ecosystems (Cole 1968; Green 1993; Green & Mengestou 1991; Hammer 1986; Walker 1981). Vareschi & Jacobs (1984), on the other hand, reported that rotifer abundance in Lake Nakuru, Kenya, was unexpectedly low. Fish were neither abundant, occurring in14% of all samples, nor widely distributed, occurring in 40% of all ponds.

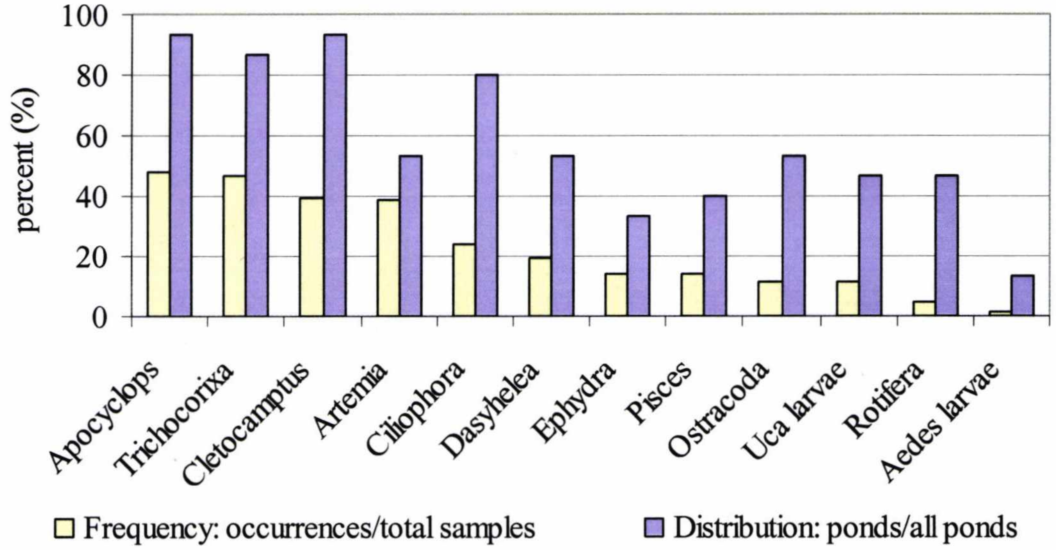


Figure 6.2 Frequency and distribution of aquatic biota

Aedes taeniorhynchus had the most restricted distribution, occurring in 13% of ponds sampled, and they were the most rarely encountered, occurring in 2% of samples. This finding refutes the commonly held local belief that salt ponds are ideal habitats for mosquito reproduction. Hypersaline ponds were normally too saline and insolated to support mosquito larvae. However, small, shaded pools among mangroves tended to collect less saline water after rainfall, providing better habitat for mosquito larvae (Nayar 1985; Walker & Newson 1996).

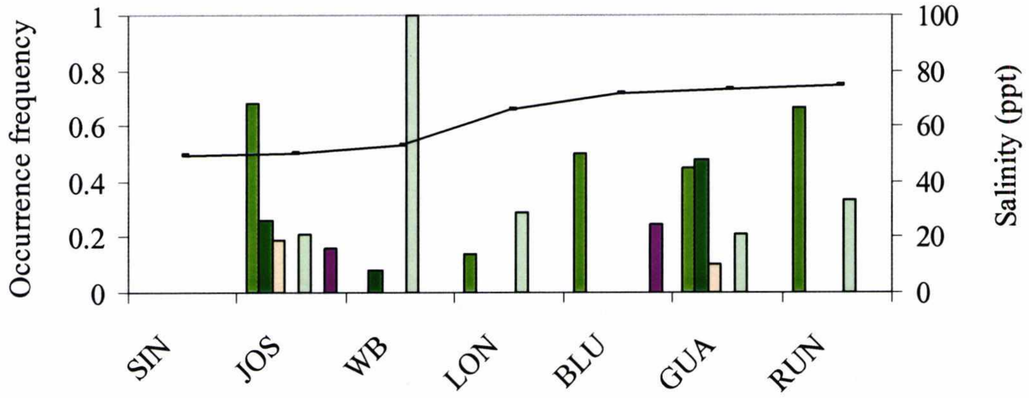
Species distributions generally showed no relationship with the permanence of water in ponds. Only *Ephydra* was consistently absent from ponds that dried seasonally, but its distribution probably reflected the type of bottom sediments and the distribution of BMCs, on which they are known to feed (Davis 1978;: Foote 1995; Herbst 1990), rather than the ability of *Ephydra* to colonize temporary ponds. Ephydrids are known to inhabit seasonally ephemeral ponds elsewhere (Herbst 1990).

Herbst (1990) showed that *Ephydra hains* in Mono Lake was least abundant in sand or sandy mud substrates. Similarly, *Ephydra gracilis* in the BVI was never observed in GUA, JOS and RUN, which had sandy mud sediments. Unlike *Ephydra hains* in Mono Lake, *Ephydra gracilis* did not require rocky substrates for pupal attachment. Pupae were attached either to a firm gelatinous bacterial layer covering the organic bottom sediments (e.g. BAN and BEL) or to a crust of calcite and gypsum that formed by precipitation at the bottom of some ponds (e.g. RED and FLA).

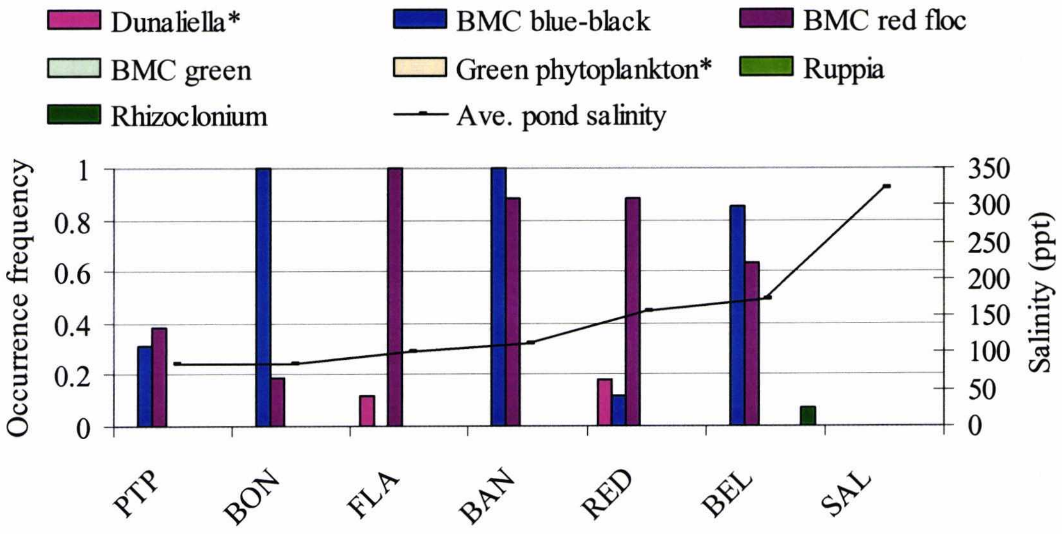
6.2 (b.*ii*) Producer communities

Producer communities showed marked differences in their distribution across ponds (Figure 6.3). Green phytoplankton blooms occurred infrequently (JOS 19% of samples and GUA 10% of samples). *Rhizoclonium* sp. was often present at low salinities, but it was rarely a dominant feature of pond communities. It occurred in JOS, WB, GUA and BEL. *Ruppia maritima* occurred regularly in lower salinity ponds (Figure 6.3(a)). It occurred frequently in JOS (68% of samples), RUN (67% of samples), BLU (50% of samples) and GUA (45% of samples).

Ruppia grew in ponds with sandy-mud sediments and mean salinities below 90 ppt. This observation was consistent with Kantrud's (1991) report that salinities greater than 70 ppt limit growth and reproduction by *Ruppia maritima*. Kantrud also reported that *Ruppia* is intolerant of loose and silty sediments, which can explain why *Ruppia* did not grow in BON or SIN, (Figure 6.3) where salinities were appropriate but sediments were loose and organic. *Rhizoclonium* and *Cladophora* were often associated with *Ruppia* meadows. This association has also been described by Kantrud (1991) in North American coastal wetlands. Green phytoplankton blooms occurred only at low salinities and in the absence of *Ruppia*. *Ruppia* is known to absorb nutrients from the water column through its leaves (Kantrud 1991), which may limit nutrients available to phytoplankton.



a) Low salinity ponds



b) High salinity ponds

Figure 6.3 Distribution of producer communities among ponds (ponds ordered by increasing mean salinity)

Green BMC was always present in WB, and it was occasionally present in JOS, LON, GUA and RUN (occurring in 21%, 19%, 21% and 33% of samples, respectively, Figure 6.3(a)). Blue-black BMC was the most common form of bacterial mat found in BVI ponds, but it never occurred in low-salinity ponds (Figure 6.3). Blue-black BMCs were present on all sampling dates in BAN and BON, and they were frequently present in BEL (85% of samples). They were observed less frequently in PTP (31% of samples) and RED (12% of samples), which was usually covered by a hard calcite/gypsum crust. Red floc was often found in association with blue-black BMC. It occurred in BAN (88% of samples), BEL (63% of samples), BON (19% of samples), PTP (38% of samples) and RED (100% of samples).

Blue-black and red floc BMCs in the BVI did not occur in the same ponds as *Ruppia maritima* (Figure 6.3). Ponds that contained blue-black and red floc BMCs rarely experienced salinities below 65 ppt. Green BMCs, in contrast, developed in ponds with lower mean salinities (GUA, JOS, LON, RUN and WB). They occurred in the same ponds as *Ruppia* but always at different times, suggesting a potential for direct competition (Des Marais 1995). Factors such as sediment composition (Guerrero *et al.* 1994; Herbst 1988; Waterman *et al.* 1999), salinity (Cornee *et al.* 1992), nutrient availability (Javor 1989), bioturbation and grazing (Bauld 1981; Burke & Knott 1997; Castenholz 1994; Fenchel 1998) were also likely to have influenced the distribution of BMCs.

Blooms of the bright red chlorophyte *Dunaliella* were seen only in RED (18% of samples) and FLA (12% of samples).

SIN and SAL showed no well-developed and easily observed producer communities, but producers were assuredly present at densities too low to permit their visual observation.

6.2 (c) Distribution and abundance of fiddler crabs

Uca burgersi (fiddler crab) burrows were most common along the shores of the low-salinity ponds WB, GUA and JOS, which had nearly 10 times more crab holes than other ponds (Table 6.2). No crab holes were ever observed at SAL. Abundance of burrows at GUA and JOS peaked in November and December (Figure 6.4(a)), presumably reflecting a seasonal pattern of reproduction as has been shown for other *Uca* species (Dittel & Epifanio 1990). *Uca* abundance at the Anegada ponds, however, peaked during February and March as well as in September (Figure 6.4(b)).

Table 6.2 Mean densities of *Uca* burrows along the shores of 10 ponds, 1995

Pond	burrows/m^2	N	Pond	burrows/m^2	N
BAN	21 ± 14	10	JOS	300 ± 50	10
BEL	21 ± 8.3	8	PTP	23 ± 13	10
BON	15 ± 7.1	9	RED	26 ± 11	11
FLA	32 ± 11	11	SAL	0	10
GUA	210 ± 54	11	WB	190 ± 35	10

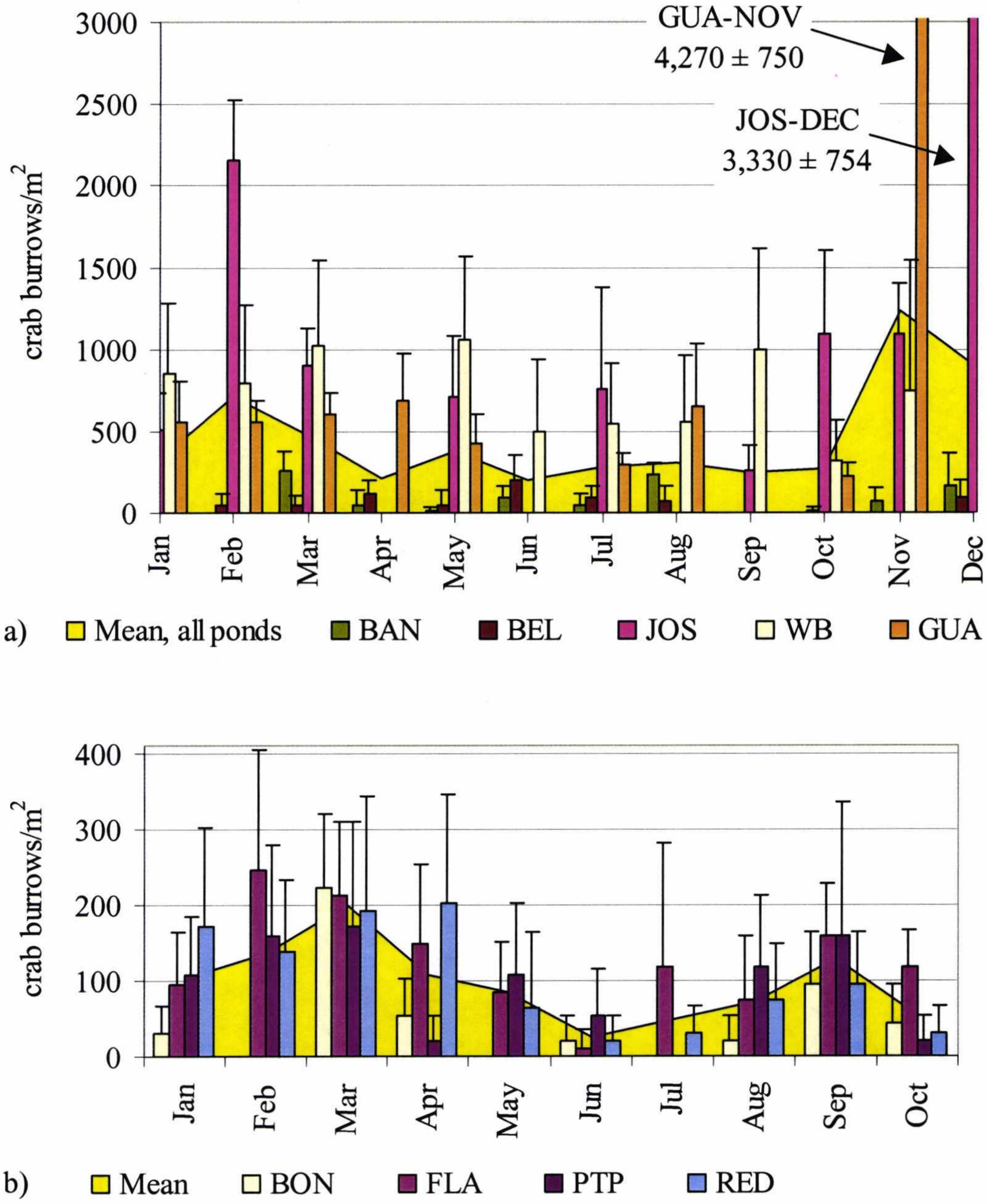


Figure 6.4 Densities of *Uca* burrows, 1995. Values shown are means of 6 replicate quadrat samples from each pond, and error bars indicate one SD above each mean.

The presence of *Uca* larvae in ponds was observed only after heavy rainfall. This sudden appearance of larvae in plankton samples may have resulted either from rains that induced a mass hatching of *Uca* eggs within ponds or from larvae being flushed into the ponds from elsewhere. The larvae, however, were already at various stages of development when they first appeared in ponds, indicating that they were flushed into the ponds from elsewhere.

Most *Uca* species are known to lay their eggs in estuaries (e.g. Dittel & Epifanio 1990), but *Uca burgersi* larvae appeared in ponds that had no connection with marine or estuarine waters. Perhaps in the BVI the eggs of *Uca burgersi* hatched within burrows of adult crabs, and when pond water level rose over the top of *Uca* burrows, the larvae washed into the ponds. The following observations support this hypothesis. *Uca* larvae appeared in plankton samples from GUA, JOS and LON immediately after they were submerged by Hurricane Georges (Figure 6.5). *Uca* holes at BAN were not submerged by Hurricane Georges because the burrows at BAN occurred high on the shore within the vegetation. As a result, *Uca* larvae did not appear in BAN until one month later (Figure 6.5) when additional rains elevated the water level above the vegetation line. These rains also raised the water levels of GUA and JOS but not of LON, since it was connected with the sea after Hurricane Georges (see Section 4.2 (a.*ii*)). Consequently, the abundance of *Uca* larvae in GUA and JOS, but not in LON, increased substantially after the second rains. Reproduction within adult burrows has not been described for any species of *Uca* (Todd Zimmerman, pers. comm. 1998). Further study of *Uca burgersi* at salt ponds may illuminate a life history unique among fiddler crabs, with the potential consequence of reproductive isolation and opportunities for speciation.

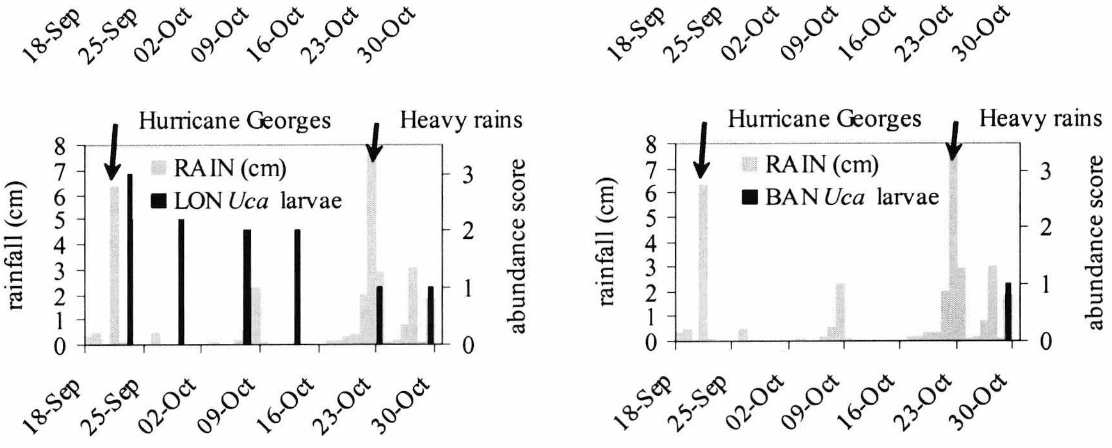


Figure 6.5 *Uca* larvae in plankton after heavy rainfall (BAN, JOS, GUA and JOS, September – October, 1998)

6.2 (d) Variation in zooplankton densities

6.2 (d.*i*) Mean zooplankton densities

Table 6.3 shows mean densities (when present) of common aquatic taxa recorded in the 10 ponds studied during 1995. *Artemia* was most abundant in BAN, with a mean density of 160 ± 500 ind/L, while in other ponds mean *Artemia* densities were between 0.77 and 5.7 ind/L. The greatest density of *Artemia* was recorded in BAN on September 4th 1995 at 1,584 ind/L, but in general, *Artemia* densities in BVI salt ponds were similar to those reported elsewhere (1.2 – 400 ind/L, Persoone & Sorgeloos 1980). *Artemia* densities in FLA and SAL were low (0.8 ind/L for both ponds), although *Artemia* occurred frequently in these ponds. *Artemia* did not occur in WB or JOS, and it did not occur in GUA prior to 1995. Elevated salinities caused by hypersaline effluents from a desalination plant combined with dry weather and a supply of *Artemia* cysts that were introduced to GUA in 1991 led to the development of a large *Artemia* population in GUA during 1995.

Trichocorixa was abundant in GUA and JOS (1.8 ± 1.7 ind/L and 1.1 ± 2.5 ind/L, respectively), while in other ponds mean *Trichocorixa* densities were less than 0.2 ind/L. Recorded population densities were lower than actual densities (not estimated) because *Trichocorixa* actively avoided the plankton net and because samples were taken near the middle of ponds where *Trichocorixa* was least abundant (personal observations and Vareschi & Vareschi 1984).

Apocyclops occurred in all ponds except RED and SAL. Mean densities measured in JOS (370 ± 280 ind/L), GUA (230 ± 120 ind/L), FLA (120 ±180 ind/L) and WB (120 ± 130 ind/L) were high compared with figures of 100 ind/L reported by Dexter (1993) for a similar species, *Apocyclops dengizicus,* in microculture. *Cletocamptus* occurred in all ponds except SAL and was most abundant in WB (130 ± 180 ind/L) and GUA (79 ± 96 ind/L) but least abundant in BEL, FLA and RED ponds. *Uca* larvae and ostracods were recorded only in JOS and WB during 1995, but observations from other years indicated wider distributions for these taxa.

Table 6.3 Mean densities (when present) of zooplankton taxa in each pond during 1995.

Species/group	**BAN** N = 12	**BEL** N = 10	**BON** N = 10	**FLA** N = 9	**GUA** N = 10
Artemia	160 ± 500	5.7 ± 8.6	4.0 ± 6.9	0.78 ± 0.93	5.5 ± 9.0
Tricochorixa	0.02 ± 0.03	0.15 ± 0.13	0.01 ± 0	0	1.8 ± 1.7
Apocyclops	3.8 ± 2.9	56 ± 60	15 ± 20	120 ± 180	230 ± 120
Cletocamptus	1.2 ± 1.0	0.48 ± 0.47	3.5 ± 4.5	0.29 ± 0.36	79 ± 96
Ostracoda	0	0	0	0	0
Uca larvae	0	0	0	0	0

Species/group	**JOS** N = 7	**PTP** N = 6	**RED** N = 10	**SAL** N = 11	**WB** N = 9
Artemia	0	1.6 ± 1.9	2.3 ± 4.7	0.77 ± 0.91	0
Tricochorixa	1.1 ± 2.5	0	0	0	0.02 ± 0.01
Apocyclops	370 ± 280	22 ± 29	0	0	120 ± 130
Cletocamptus	23 ± 30	3.0 ± 1.7	0.35 ± 0.52	0	130 ± 180
Ostracoda	0	0	0	0	0.98 ± 1.3
Uca larvae	4.9 ± 6.6	0	0	0	0.01 ± 0

Sampling during 1995 (Table 6.3) and other years showed that aquatic taxa were widely distributed across the BVI. All taxa were recorded from islands with more than one sampled pond (Anegada, Beef Island, and Tortola). Wide distributions across ponds imply that salt pond taxa are not limited by dispersal (see also Section 1.5 (b)).

6.2 (d.*ii*) Faunal shifts

Populations of aquatic taxa became established, died out, and re-established multiple times within ponds during 1995 (Figure 6.6). *Artemia*, for example, was found throughout 1995, but the longest a single pond maintained a continuous population of *Artemia* was 8 months (BAN, Figure 6.6(a) and GUA, Figure 6.6(e)). The longest-lived population of *Trichocorixa* lasted for only 4 months (GUA, Figure 6.6(e)). *Apocyclops* and *Cletocamptus* disappeared and later reappeared in most ponds, as did *Ephydra* and *Dasyhelea* in some ponds.

Early in the year, all 10 ponds sampled were inundated, but salinities varied from 38 ppt (WB) to 300 ppt (SAL). *Artemia* was present in ponds with salinities greater than

100 ppt (BAN, BEL, RED and SAL, Figure 6.6(a, b, h & i)). *Ephydra* was also present in BAN, BEL and RED, and *Cletocamptus* was present in BAN. These populations persisted with an occasional loss (e.g. *Ephydra* in BAN during March & April) or gain (e.g. *Apocyclops* in BAN and *Cletocamptus* in RED during April) of a taxon. All taxa disappeared, however, when salinities approached 300 ppt (SAL, April – July, and BEL, April).

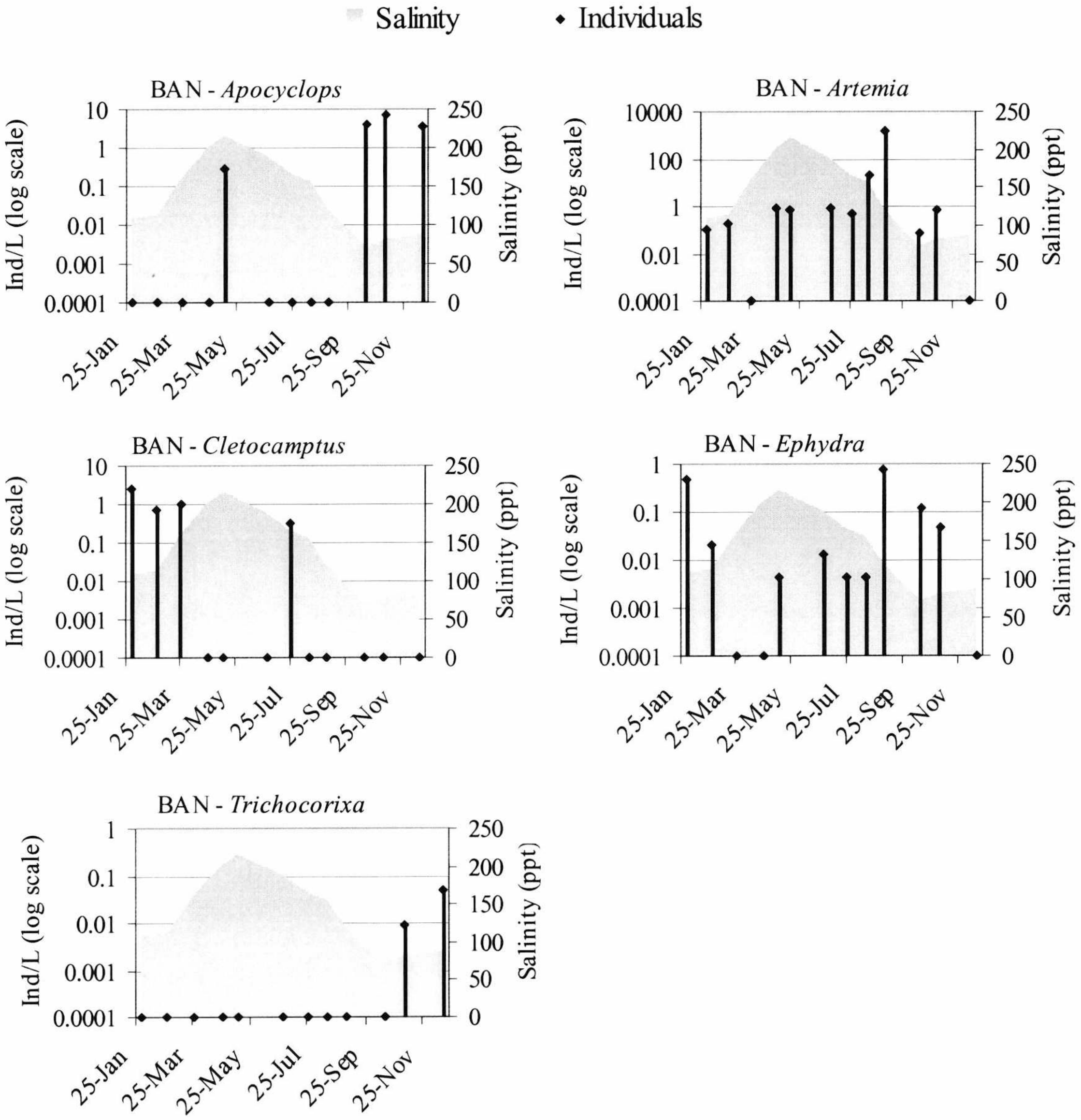


Figure 6.6 (a) Population fluctuations of aquatic taxa in BAN 1995

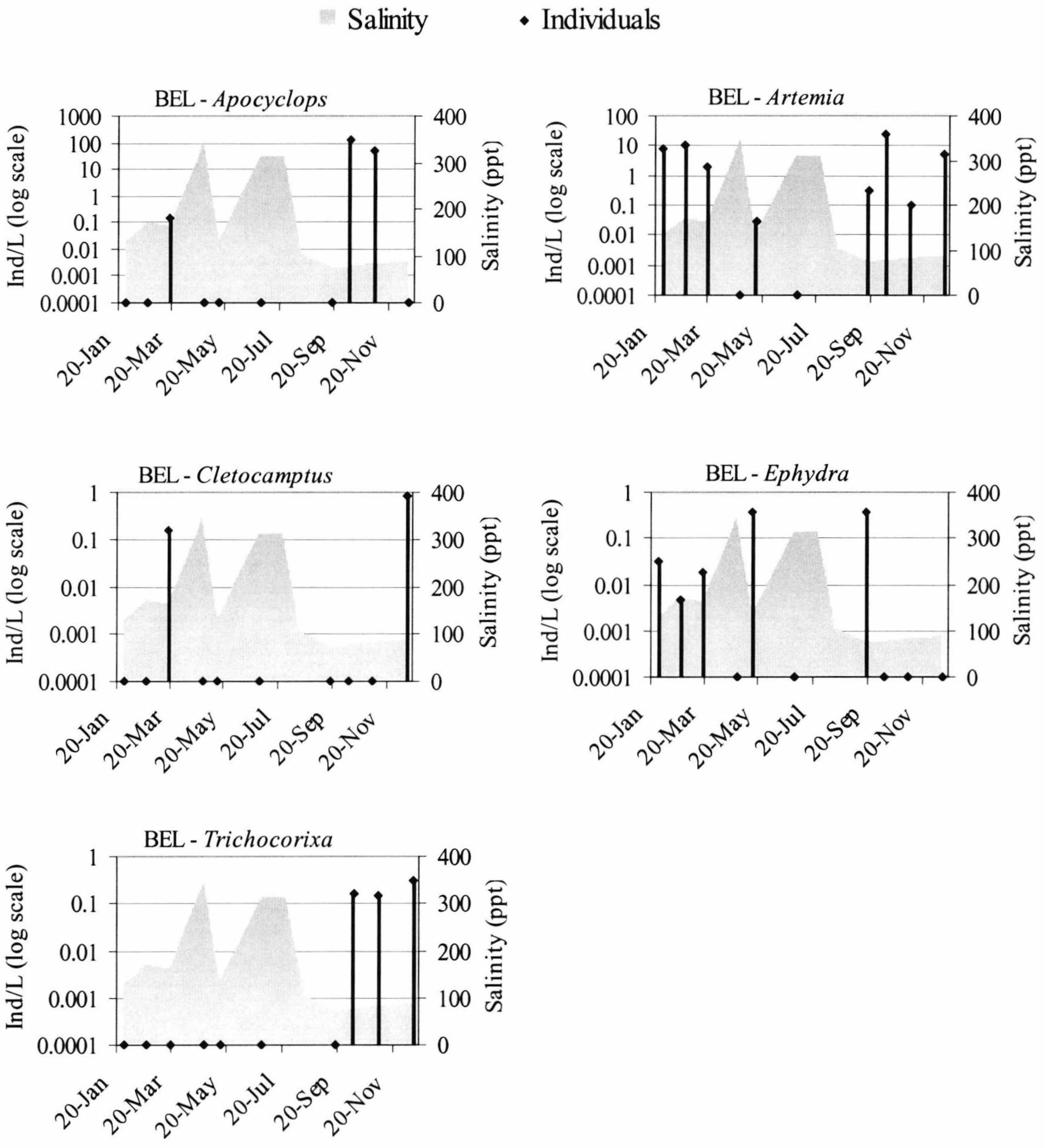


Figure 6.6 (b) Population fluctuations of aquatic taxa in BEL during 1995

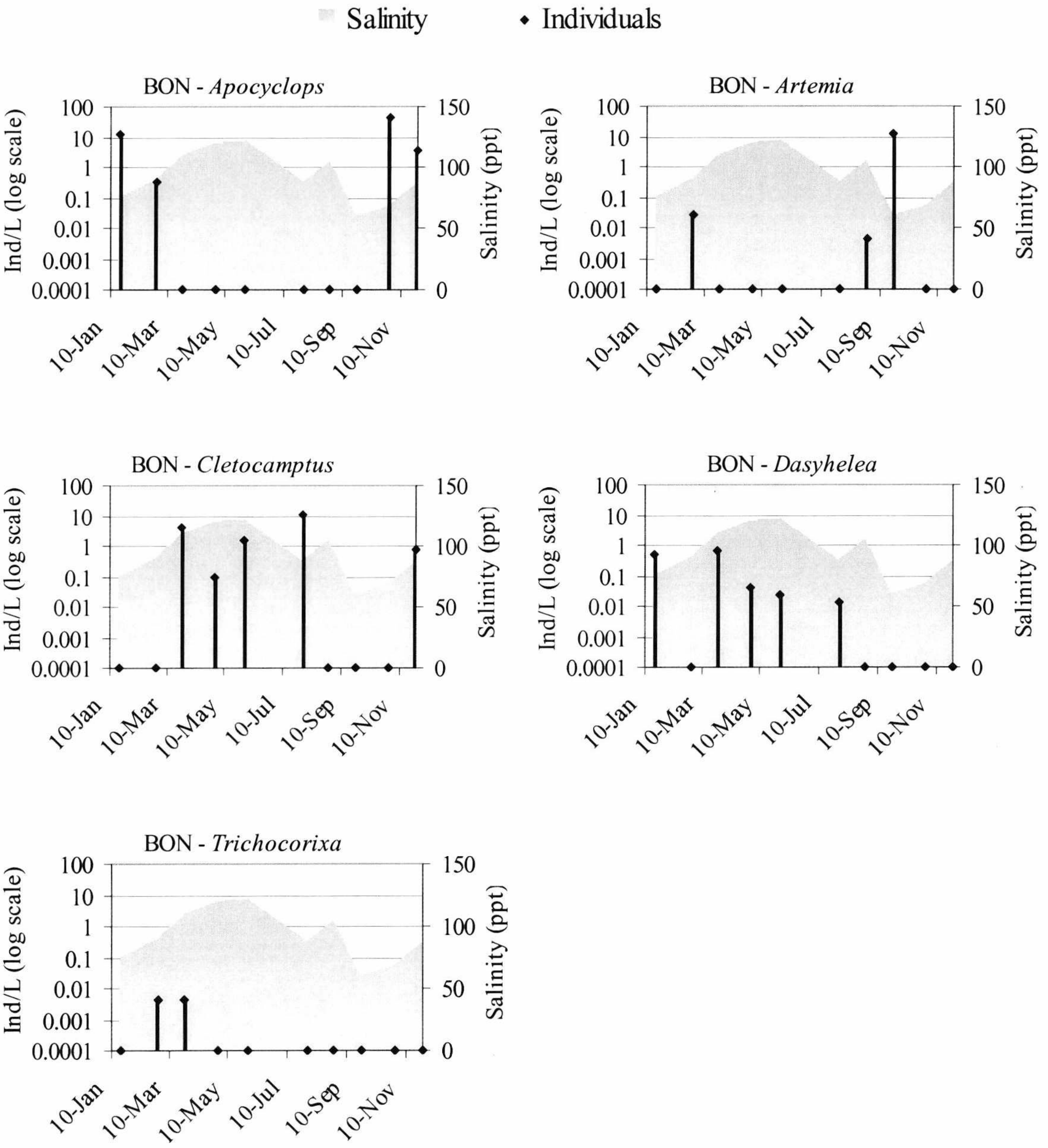


Figure 6.6 (c) Population fluctuations of aquatic taxa in BON during 1995

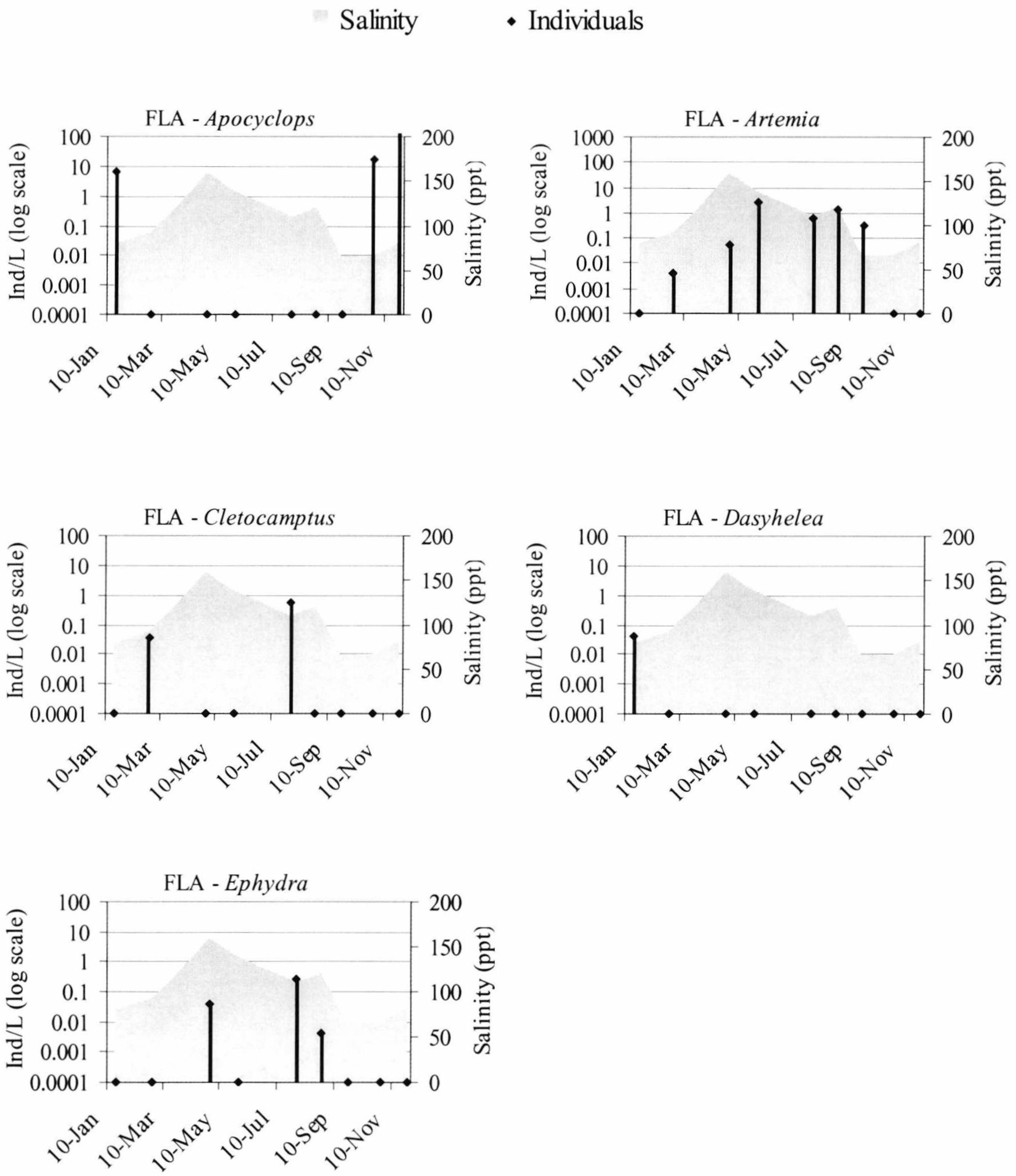


Figure 6.6 (d) Population fluctuations of aquatic taxa in FLA during 1995

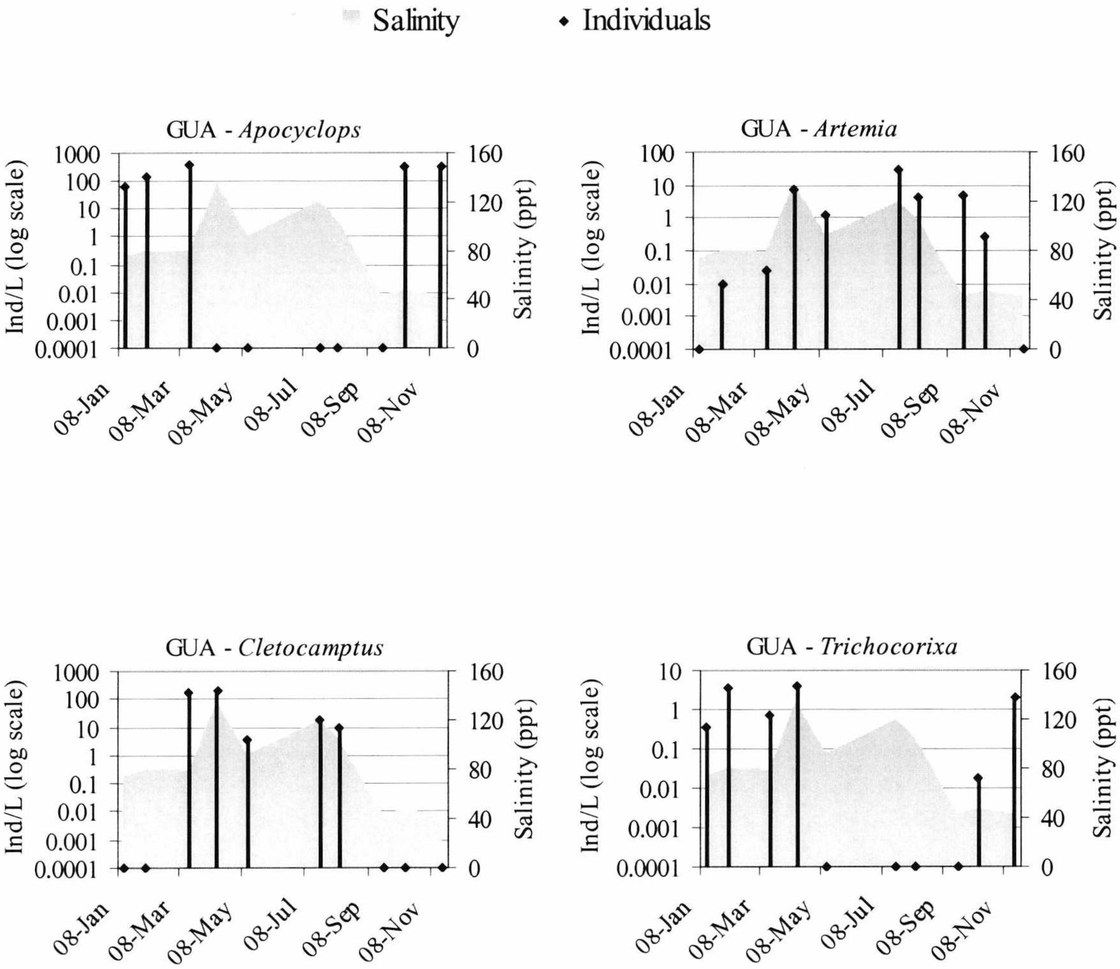


Figure 6.6 (e) Population fluctuations of aquatic taxa in GUA during 1995

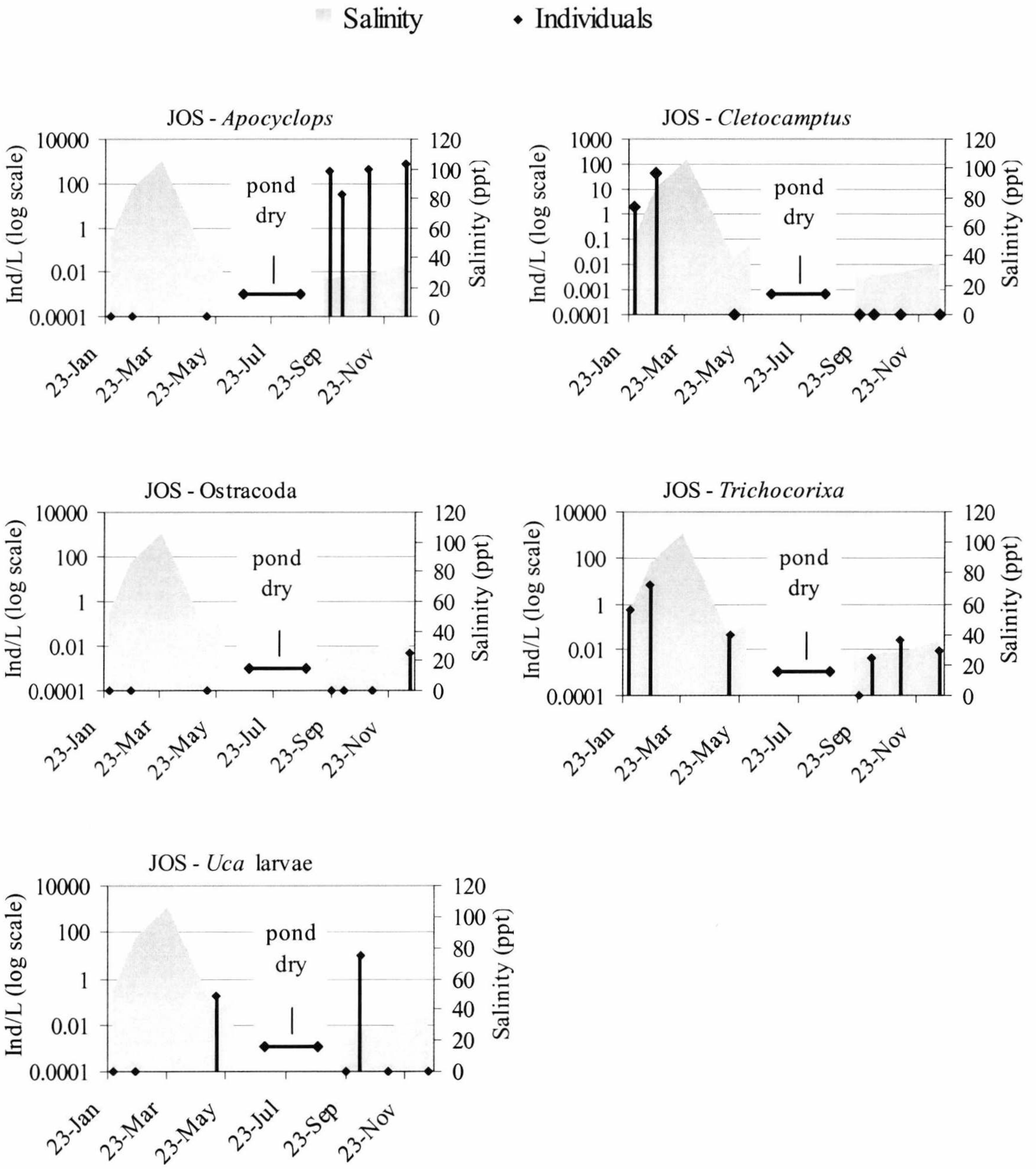


Figure 6.6 (f) Population fluctuations of aquatic taxa in JOS during 1995

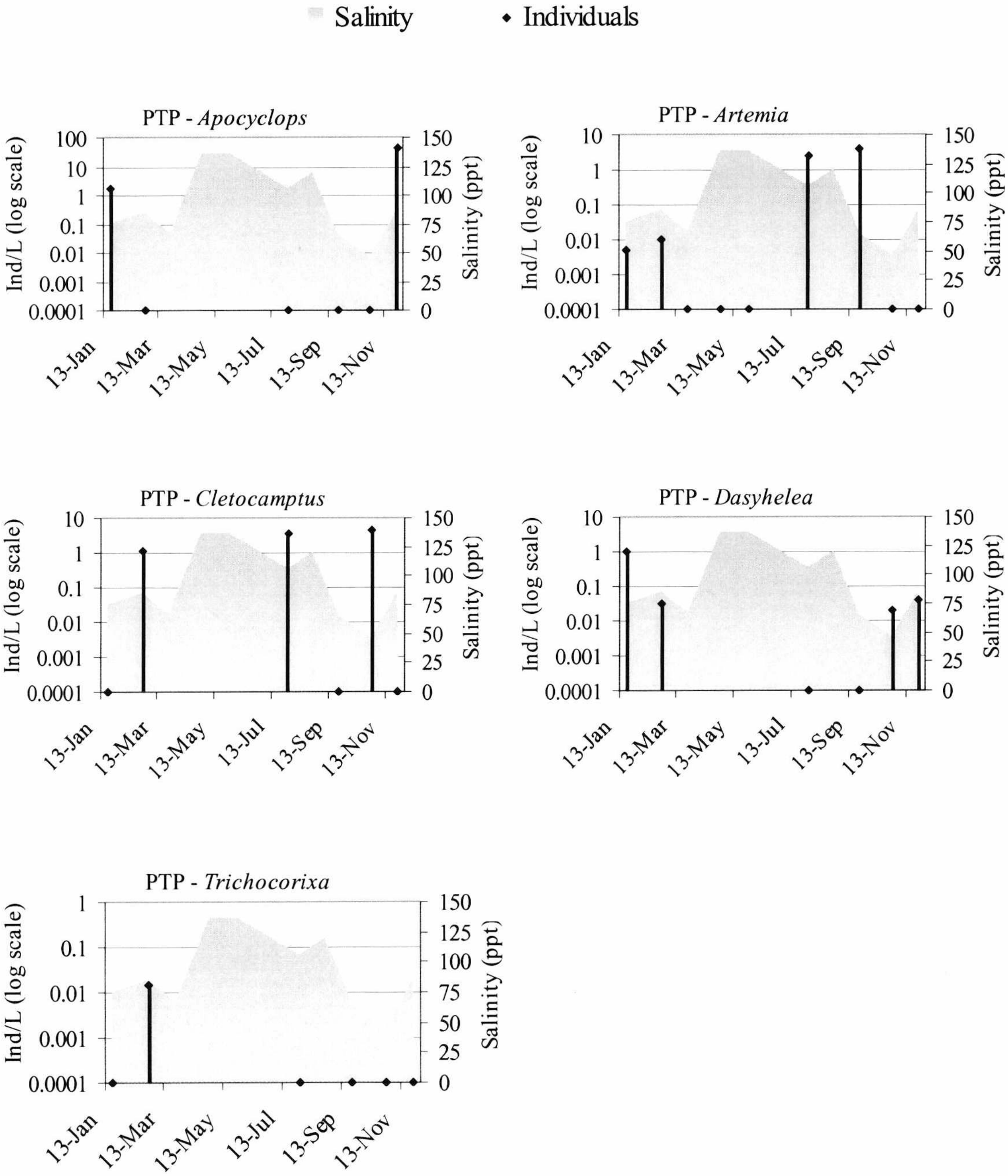


Figure 6.6 (g) Population fluctuations of aquatic taxa in PTP during 1995

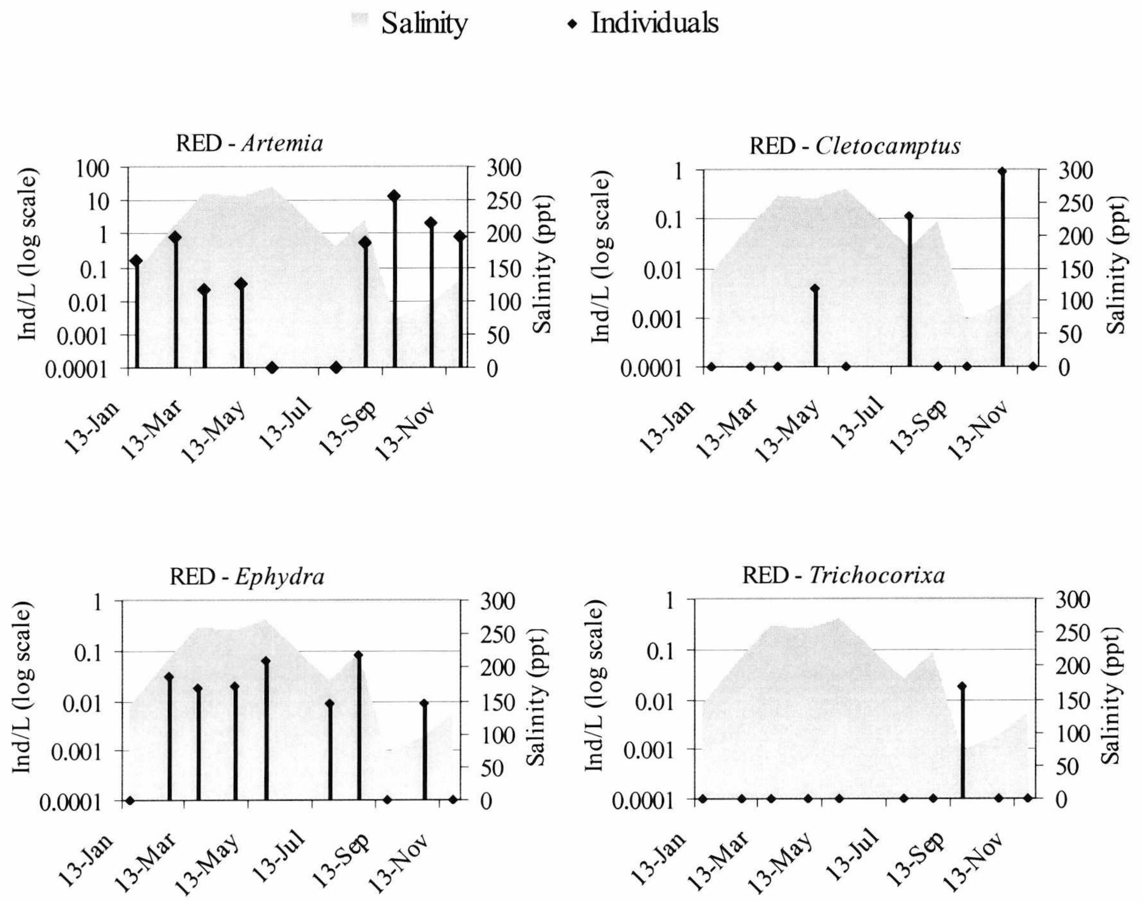


Figure 6.6 (h) Population fluctuations of aquatic taxa in RED during 1995

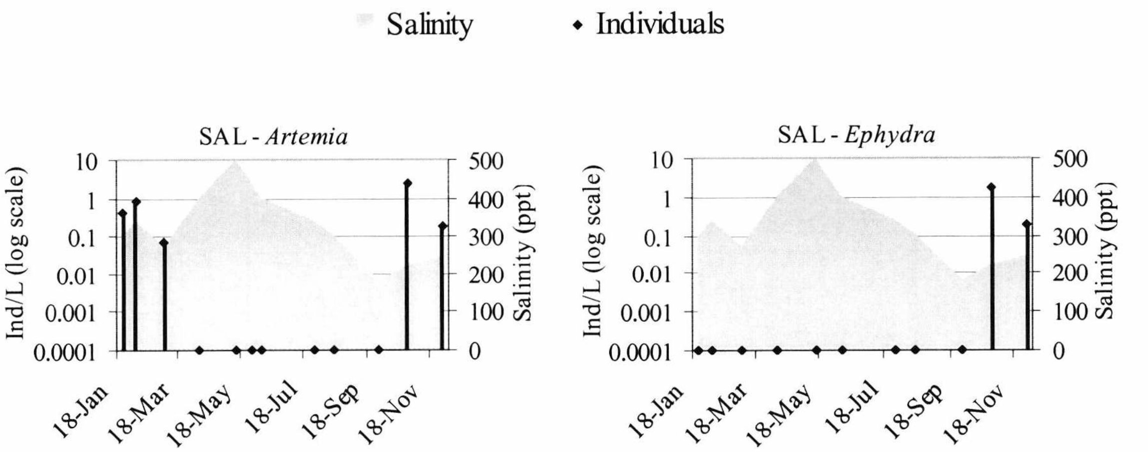


Figure 6.6 (i) Population fluctuations of aquatic taxa in SAL during 1995

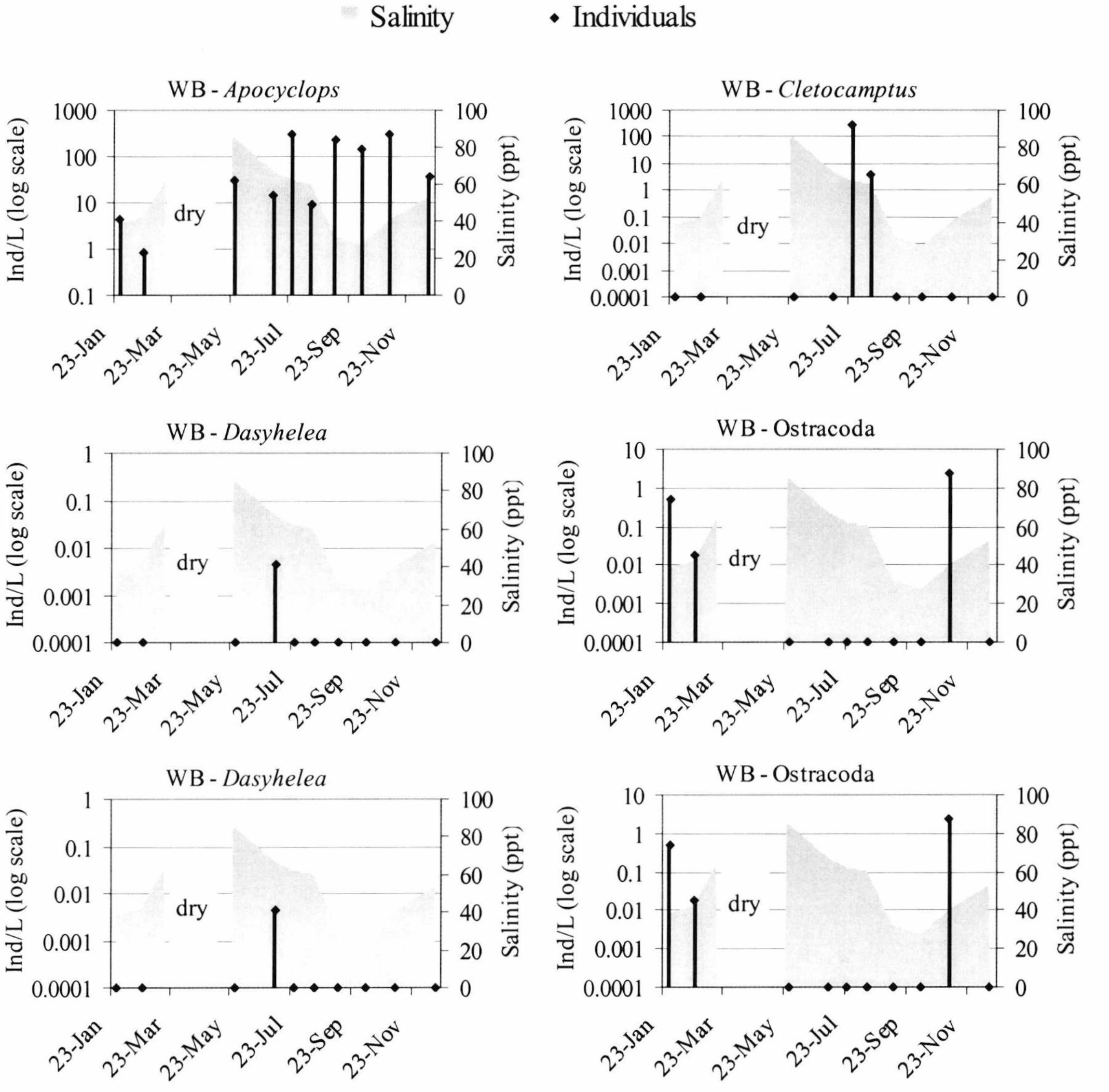


Figure 6.6 (j) Population fluctuations of aquatic taxa in WB during 1995

Ponds having salinities lower than 100 ppt early in the year (BON, FLA, GUA, JOS, PTP and WB, Figure 6.6(c - g, j)) generally supported combinations of *Apocyclops* (BON, FLA, GUA, PTP and WB), *Trichocorixa* (BON, GUA, JOS, PTP and WB), and occasionally *Dasyhelea* (BON, FLA and PTP) and/or *Cletocamptus* (FLA, JOS, PTP). Of these, ponds with salinities greater than 75 ppt also contained or soon developed populations of *Artemia* (BON, FLA, GUA and PTP). Ostracods were present in WB, which maintained salinities below 40 ppt for the first 2 months of 1995.

Dry conditions from February through July caused the complete disappearance of *Apocyclops, Dasyhelea,* ostracods and *Trichocorixa* by the middle of the year (June) from all ponds except WB, which was filled with seawater in May (see Section 4.2 (a.*ii*)). The long dry season of 1995 broke with 2 consecutive hurricanes, both in September. Rains filled ponds and caused dramatic reductions in salinity (see Section 5.2 (a.*i*)). *Apocyclops* and/or *Trichocorixa* replaced the predominant *Artemia* and *Ephydra* populations in BAN, BON, FLA, GUA and PTP within 2 months after these rains (Figure 6.6(a, c - e & g)). After the September rains, populations of *Dasyhelea* returned to PTP. *Apocyclops*, *Trichocorixa* and ostracods recolonized JOS and WB, which were desiccated at the height of the dry season. *Artemia* and/or *Cletocamptus* populations remained in BEL, BON and RED, which quickly regained high salinities (>85 ppt) after the hurricanes. In SAL the September rains allowed *Artemia* and *Ephydra* to colonize where salinities were previously too high to support life (Figure 6.6(i)).

6.2 (e) Effects of salinity on presence or absence of taxa

6.2 (e.*i*) Results of logistic regression analyses

Logistic regression (Section 3.4 (e)) was effective not only in determining the importance of salinity in controlling the occurrence of taxa but also in modelling the range of salinities at which each taxon was likely to occur. Because logistic regression analysis was based solely on nominal data (presence and absence observations), sampling errors associated with abundance estimates did not affect the results. This method worked well for common species that developed large populations. Taxa with low population densities and taxa that were difficult to detect in samples, such as ciliates and rotifers, were problematic due to the likelihood of false negatives in the data. All taxa included in this analysis developed high population densities. Uncommon taxa, such as rotifers and ostracods, presented an additional difficulty in that the number of absence records was disproportionately large, making probability of occurrence difficult to predict. The occurrence of uncommon taxa may depend on several fortuitous environmental events rather than being limited primarily by salinity.

Results of logistic regression analyses are shown in Table 6.4. Salinity was a highly significant factor controlling the occurrence of each aquatic taxon tested. The whole-model test results showed that the probability of occurrence for each taxon changed with increasing salinity. Presence/absence data for *Apocyclops*, Ciliophora, Ostracoda, Pisces, Rotifera and *Trichocorixa* significantly fit the regression model using salinity as the only regressor. These taxa showed sigmoid relationships to increasing salinity, indicating that occurrence of the taxa was not limited at low salinities (Figure 6.7(a, c, g – j)), though salinities below that of seawater, 35 ppt, were not included in the model.

A quadratic model (using both salinity and its square as regressors) rather than a linear model was required to fit the presence/absence distributions of *Artemia, Dasyhelea* and *Ephydra* (Table 6.4). Occurrence of these taxa was limited at both low and high salinities (Figure 6.7(b, e, f)). The probability of occurrence for *Artemia, Dasyhelea* and *Ephydra* declined at low salinities ($p < 0.3$ at 80 ppt, 48 ppt and 122 ppt, respectively. The probability of occurrence for *Cletocamptus* decreased at both high and low salinities, but it remained likely to occur ($p > 0.3$) down to 35 ppt (Figure 6.7(d)). A lack of fit ($p = 0.002$ for a single regressor and $p = 0.003$ for both salinity regressors, Table 6.4) of both the sigmoid and quadratic regression models to presence/absence data for *Cletocamptus* indicated that additional information was necessary to explain the distribution of this genus.

6.2 (e.*ii*) Probable occurrence predictions

Salinity ranges at which taxa occurred generally agreed with observations from other studies. *Artemia, Cletocamptus* and *Ephydra* were the only taxa likely to occur above 130 ppt (Figure 6.8). *Artemia* was likely to occur between 80 and 314 ppt, though it survived in ponds at both higher and lower salinities. Kristensen & Hulsher-Emeis (1972) noted the presence of *Artemia* in salterns of Curacao between 45 and 360 ppt. Nixon (1970) found *Artemia* in Puerto Rican salt ponds as high as 350 ppt. *Cletocamptus* was predicted to occur up to 189 ppt, higher than that recorded for harpacticoids (32 – 113 ppt) by Kristensen & Hulsher-Emeis (1972) in salterns of Curacao but lower than that (300 ppt) reported for *Cletocamptus* worldwide by Hammer (1986). *Ephydra* were likely to occur between 122 and 185 ppt, while *Dasyhelea* were likely to occur at lower salinities. Kristensen & Hulsher-Emeis (1972), however, reported *Ephydra* at salinities down to 36 ppt in Curacao, where *Dasyhelea* was apparently absent.

Table 6.4 Statistical outputs of logistic regression analyses. “S” in column headings refers to a linear regression model using salinity as the sole regressor, while “S, S^2” refers to a quadratic model using both salinity and salinity^2 as regressors.

Whole Model Test	***Apocyc* S**	***Artemia* S**	***Artem* S, S^2**	***Cletocmpt* S**
-log likelihood*	29.7270	2.1533	17.3425	2.7757
Prob>Chi^2	0.0001	0.0380	0.0001	0.0185
R square	0.2576	0.0216	0.1738	0.0245
Observations	167	144	144	166
Lack of Fit				
-log likelihood*	85.6658	97.6040	82.4150	110.5460
Prob>Chi^2	0.3517	0.0021	0.0830	0.0020
Parameter Estim.				
Intercept	-3.2638	0.6740	5.0379	-0.4000
Salinity (S)	0.0366	-0.0052	-0.0719	0.0068
Salinity^2 (S^2)			0.0002	
Effect Test				
Wald (S)	29.6265	4.0360	25.3637	4.8396
Wald (S^2)			22.2742	
Prob>Chi^2 (S)	0.0000	0.0445	0.0000	0.0278
Prob>Chi^2 (S^2)			0.0000	

Whole Model Test	***Cleto* S, S^2**	**Cilioph S**	***Dasyh* S**	***Dasyh* S, S^2**
-log likelihood	5.2846	2.1486	3.2679	9.5006
Prob>Chi^2	0.0051	0.0382	0.0106	0.0001
R square	0.0466	0.0229	0.0505	0.1467
Observations	166	162	100	100
Lack of Fit				
-log likelihood*	108.0368	91.5948	61.4770	55.2400
Prob>Chi^2	0.0034	0.1011	0.0449	0.1650
Parameter Estim.				
Intercept	1.1681	0.3001	-0.6459	6.2648
Salinity (S)	-0.0228	0.0072	0.0128	-0.1409
Salinity^2 (S^2)	0.0001			0.0008
Effect Test				
Wald (S)	2.1880	3.5509	5.2583	6.5219
Wald (S^2)	3.2379			7.1400
Prob>Chi^2 (S)	0.1391	0.0595	0.0218	0.0107
Prob>Chi^2 (S^2)	0.0720			0.0075

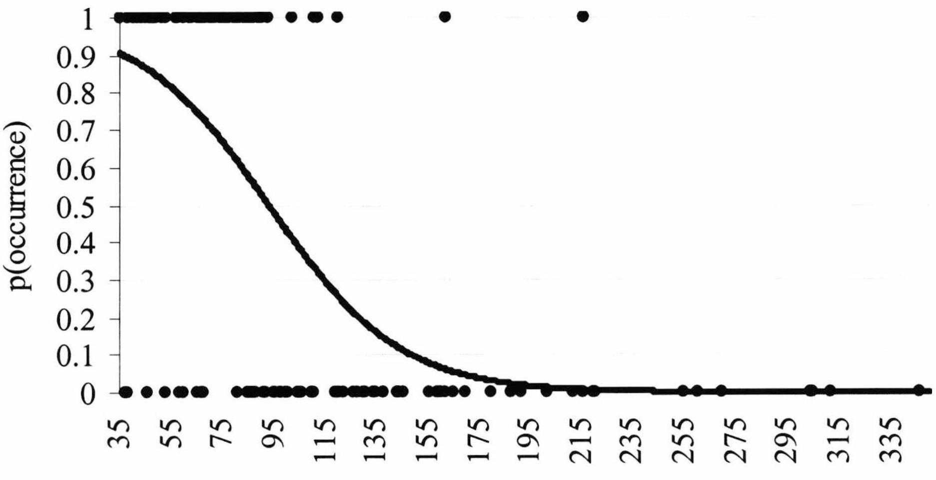
* reported value is the difference in the log likelihood from the model fitted by the data and the model with equal probabilities (background uncertainty when the model has no effects).

Table 6.4 (continued) Statistical outputs of logistic regression analyses. S in the column heading refers to a linear regression model using salinity as the sole regressor, while S, S^2 refers to a quadratic model using both salinity and salinity^2 as regressors.

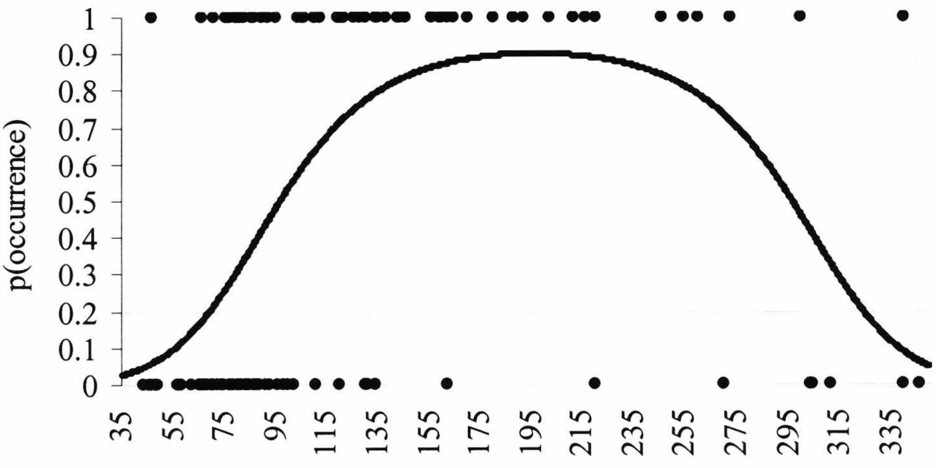
Whole Model Test	***Ephydra*** **S**	***Ephy*** **S, S^2**	**Ostracod S**	**Pisces S**
-log likelihood*	1.7563	5.9731	5.4665	6.5429
Prob>Chi^2	0.0609	0.0025	0.0009	0.0003
R square	0.0341	0.1160	0.1059	0.1588
Observations	85	85	101	68
Lack of Fit				
-log likelihood*	49.7365	45.5197	46.1636	34.6513
Prob>Chi^2	0.1050	0.2318	0.6692	0.3667
Parameter Estim.				
Intercept	1.7521	5.5200	-1.2031	-2.2325
Salinity (S)	-0.0057	-0.0541	0.0350	0.4098
Salinity^2 (S^2)		0.0001		
Effect Test				
Wald (S)	3.4750	8.5526	8.5393	9.3085
Wald (S^2)		7.0885		
Prob>Chi^2 (S)	0.0623	0.0035	0.0035	0.0023
Prob>Chi^2 (S^2)		0.0078		

Whole Model Test	**Rotifera S**	***Trichocorixa*** **S**	***Uca*** **larvae S**
-log likelihood*	5.3861	28.8305	15.3624
Prob>Chi^2	0.0010	0.0001	0.0001
R square	0.1828	0.2510	0.3330
Observations	92	166	103
Lack of Fit			
-log likelihood*	24.0797	86.0390	30.7760
Prob>Chi^2	0.9999	0.3172	0.9993
Parameter Estim.			
Intercept	-1.0407	-3.1586	-3.2851
Salinity (S)	0.0425	0.0348	0.0722
Salinity^2 (S^2)			
Effect Test			
Wald (S)	5.5770	29.2397	14.0540
Wald (S^2)			
Prob>Chi^2 (S)	0.0182	0.0000	0.0002
Prob>Chi^2 (S^2)			

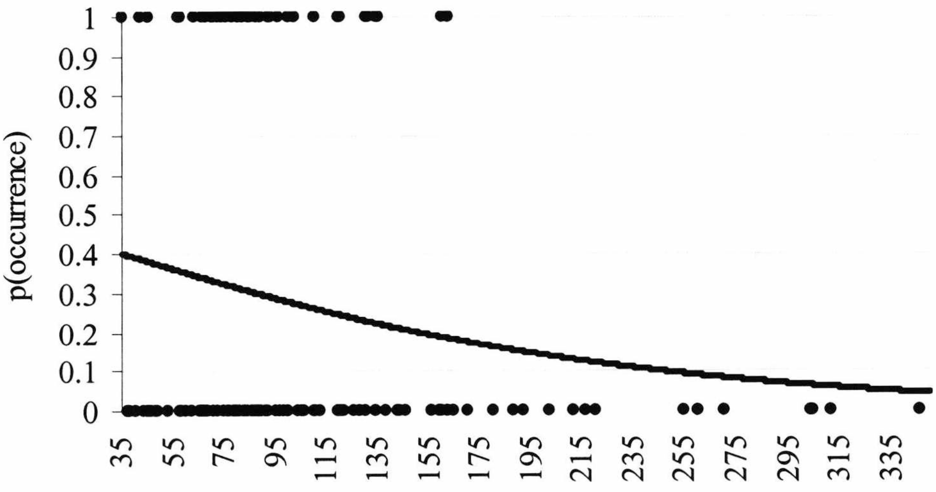
*reported value is the difference in the log likelihood from the model fitted by the data and the model with equal probabilities (background uncertainty when the model has no effects).



a) *Apocyclops dengizicus*

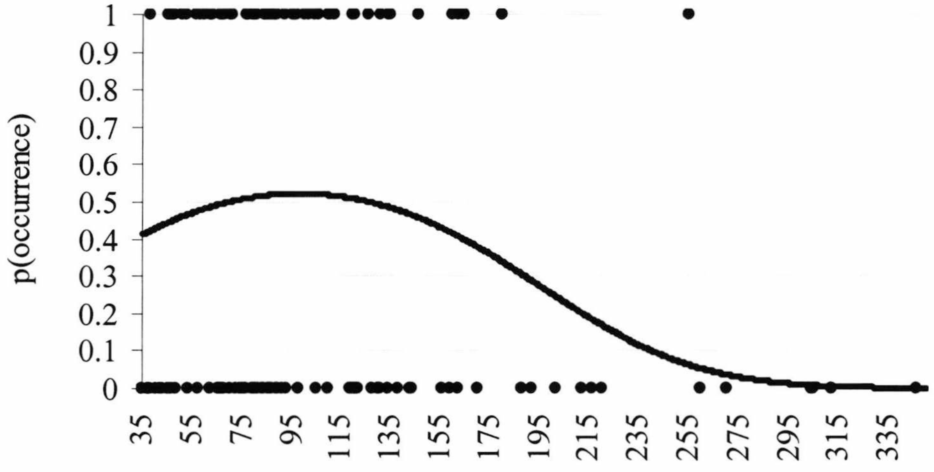


b) *Artemia franciscana*

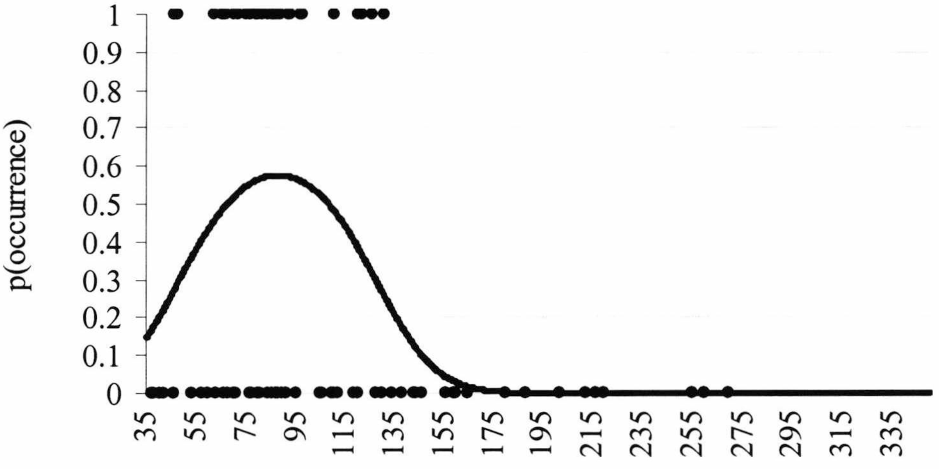


c) Ciliophora

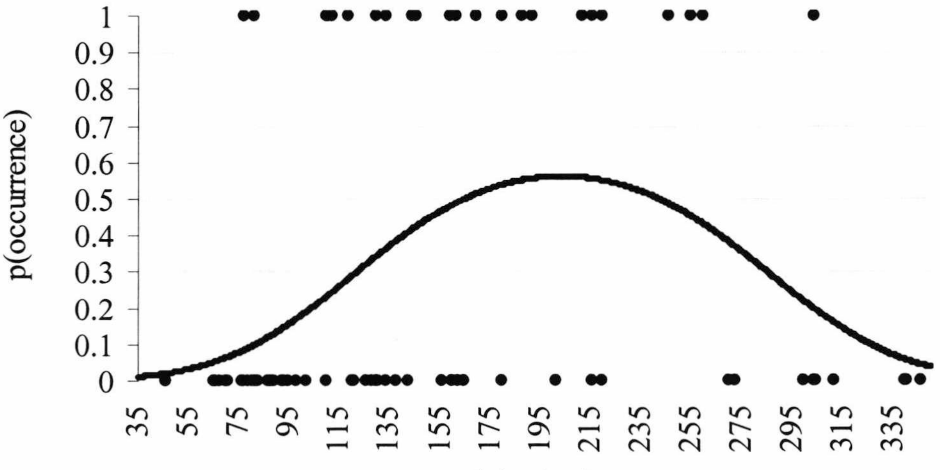
Figure 6.7 Probability of occurrence (shown as a curve) predicted by logistic regression of presence/absence data (shown as points)



d) *Cletocamptus*

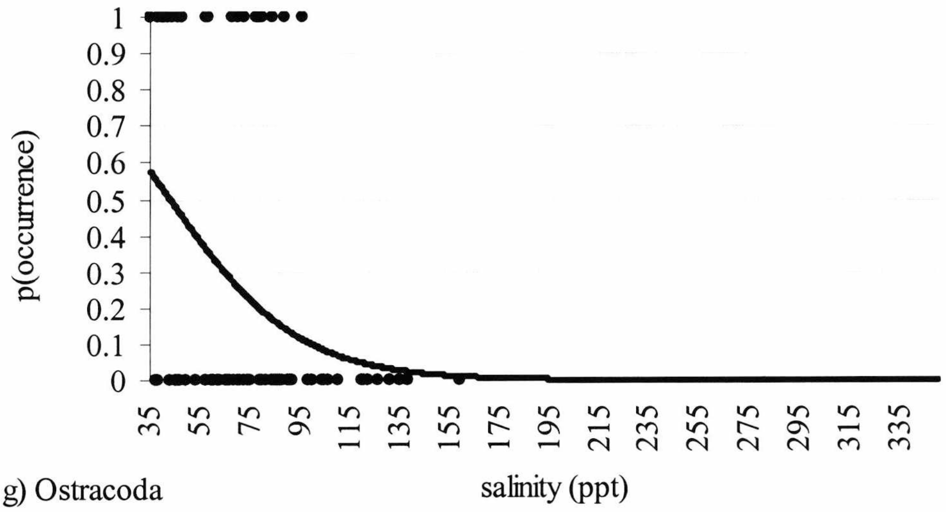


e) *Dasyhelea*

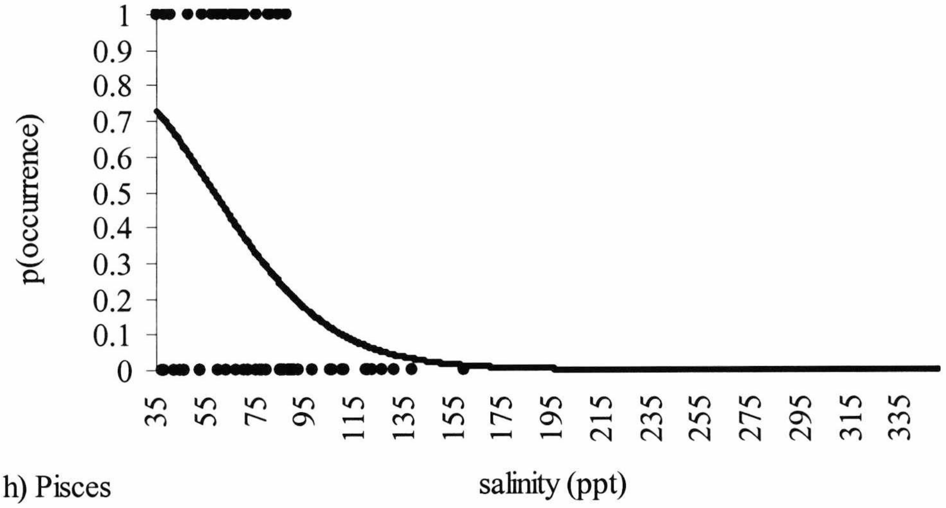


f) *Ephydra gracilis*

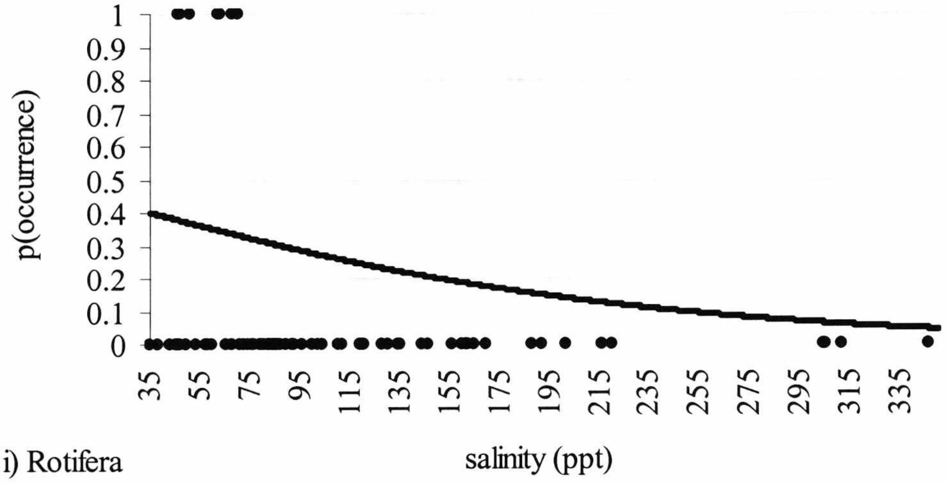
Figure 6.7 (continued) Probability of occurrence (shown as a curve) predicted by logistic regression of presence/absence data (shown as points)



g) Ostracoda

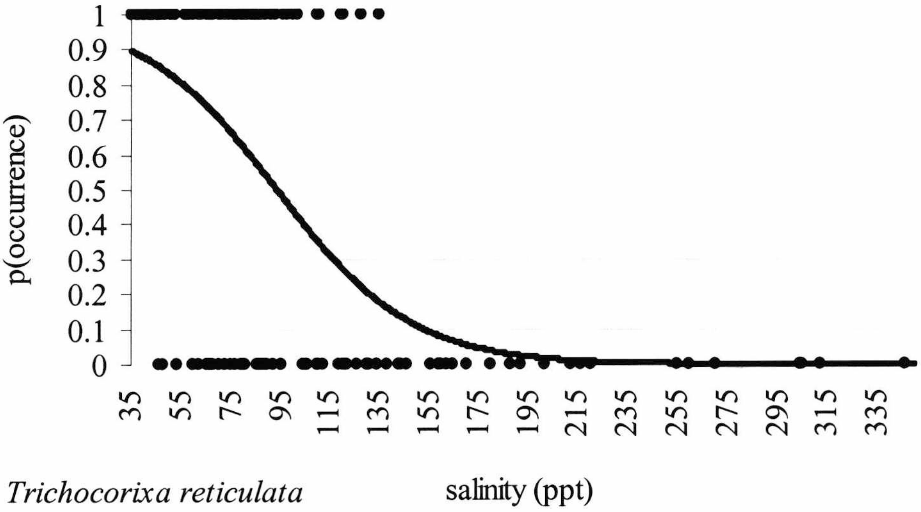


h) Pisces



i) Rotifera

Figure 6.7 (continued) Probability of occurrence (shown as a curve) predicted by logistic regression of presence/absence data (shown as points)



j) *Trichocorixa reticulata*

Figure 6.7 (continued) Probability of occurrence (shown as a curve) predicted by logistic regression of presence/absence data (shown as points)

Occurrence of *Apocyclops panamensis* was most probable at salinities below 115 ppt (Figure 6.8). *A. panamensis* in BVI ponds showed tolerance to salinities higher than that reported for its sibling species, *A. dengizicus,* which fails to reproduce above 68 ppt and is killed at 73 ppt in microculture (Dexter 1993). *A. panamensis* nauplii were observed in BVI ponds up to 93 ppt, indicating reproduction at much higher salinities than that reported for *A. dengizicus*.

Trichocorixa was likely to occur at salinities up to 116 ppt (Figure 6.8), though it was found up to 135 ppt (Figure 6.7(j)). Hart *et al.* (1998), in contrast, reported reproduction in *Trichocorixa* at salinities up to 148 ppt. Ciliates were found occasionally at salinities as high as 162 ppt (Figure 6.7(c)), a value higher than that (100 ppt) reported by Hammer (1986). However, ciliates were predicted by logistic regression to occur only up to 87 ppt. This large difference between the highest recorded salinity at which ciliates were found and the highest salinity at which their occurrence is probable results from a high proportion of absence records at high salinities.

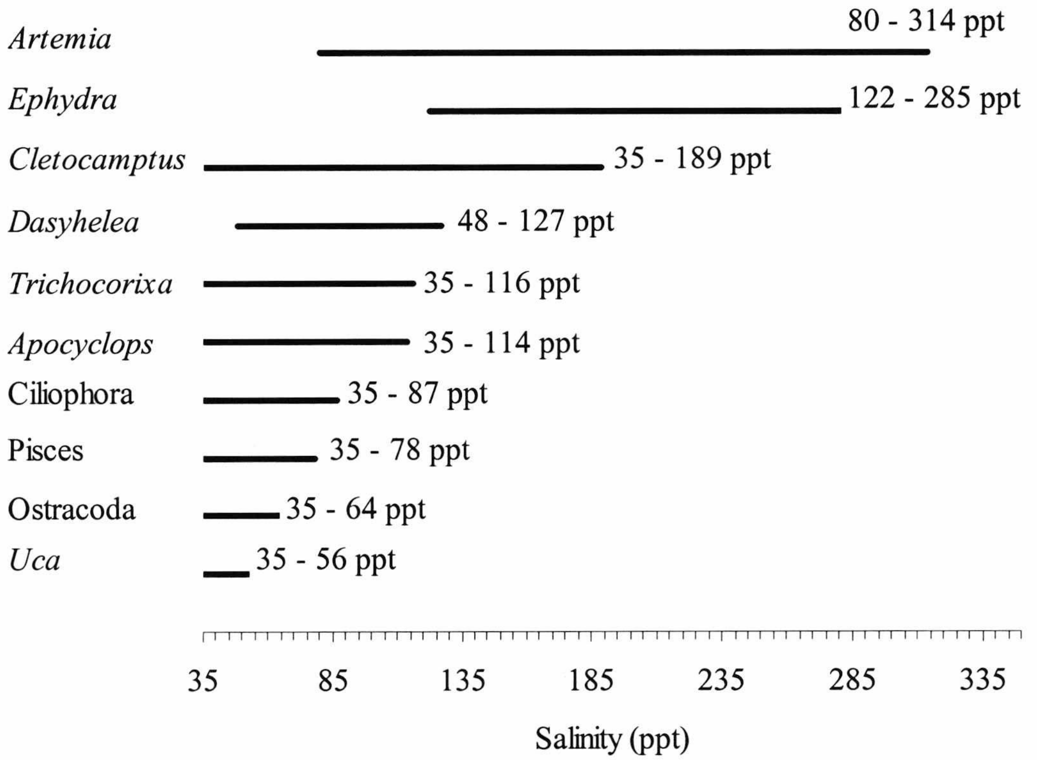


Figure 6.8 Predicted salinity ranges for each taxon as modelled by logistic regression

Rotifers, which have been reported from waters with salinities up to 145 ppt (Hammer 1993), were not found in BVI ponds at salinities higher than 70 ppt (Figure 6.7(i)). These results are based on only 8 positive occurrences, and an understanding of rotifer distribution in the BVI clearly requires additional sampling.

Fish were likely to occur only at salinities below 78 ppt, and this finding agreed with those of Gunter (1967) for similar species in Laguna Madre, Texas.

6.2 (e.*iii*) Salinity distribution of *Cletocamptus albuquerquensis* and *C. deitersi*

Specific analysis of 11 samples containing *Cletocamptus* showed that *C. albuquerquensis* and *C. deitersi* did not occur together. *C. albuquerquensis* was prevalent at salinities above 63 ppt and *C. deitersi* below 63 ppt (Figure 6.9), and this distinction was significant (Student's $t = 2.26$, $p = 0.05$, d.f. $= 9$). The single occasion on which *C. albuquerquensis* was observed at a lower salinity occurred just after a dilution event (see Figure 6.11(c)). Like other taxa, these species were not geographically separated, as each was observed in JOS at different times.

Dexter (1995) reported that the survival of *C. deitersi* was limited in microculture at salinities above 80 ppt. *C. albuquerquensis*, on the other hand, has been reported from saline waters up to 125 ppt (Hammer 1993). Grouping these 2 species in the logistic regression analysis adversely affected the model (Section 6.2 (e.*i*)) because they have different salinity limitations. The model will be improved by distinguishing *Cletocamptus* species in future samples, on which regression analyses can be performed independently for each species.

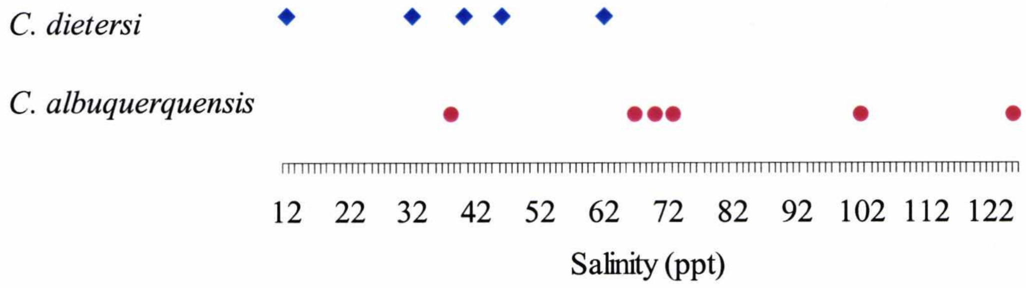


Figure 6.9 Distribution of *Cletocamptus albuquerquensis* and *C. deitersi* occurrences across salinity

6.2 (f) Effects of hurricanes and other rainfall events on aquatic fauna

6.2 (f.*i*) Hurricanes Luis and Marilyn, 1995

Turnovers in species composition generally occurred when pond salinities either increased or decreased to about 75 ppt. After Hurricanes Luis and Marilyn in 1995, salinity dropped in BAN from 120 ppt to 60 ppt, crossing this threshold. BAN initially held a high-salinity community consisting of *Artemia* and *Ephydra*, which became less abundant immediately after the hurricanes (Figure 6.10). It was expected that abrupt dilution brought on by hurricane rains would cause plankton kills and subsequent replacement by colonizing species better adapted to living at lower salinities. Contrary to this expectation, however, high-salinity taxa remained in BAN for 6 weeks after massive dilutions and before species turnover was completed. This illustrated a great tolerance by high-salinity species to abrupt changes in salinity, a tolerance that was first reported for hypersaline species nearly a century ago (Vorheis 1917).

The post-hurricane decline in *Artemia* and *Ephydra* was possibly due to mortality caused by the abrupt change in osmotic potential or to an apparent reduction in density due to a higher pond volume, or to a combination of both. Ten days after the second hurricane, *Artemia* and *Ephydra* population densities stabilized.

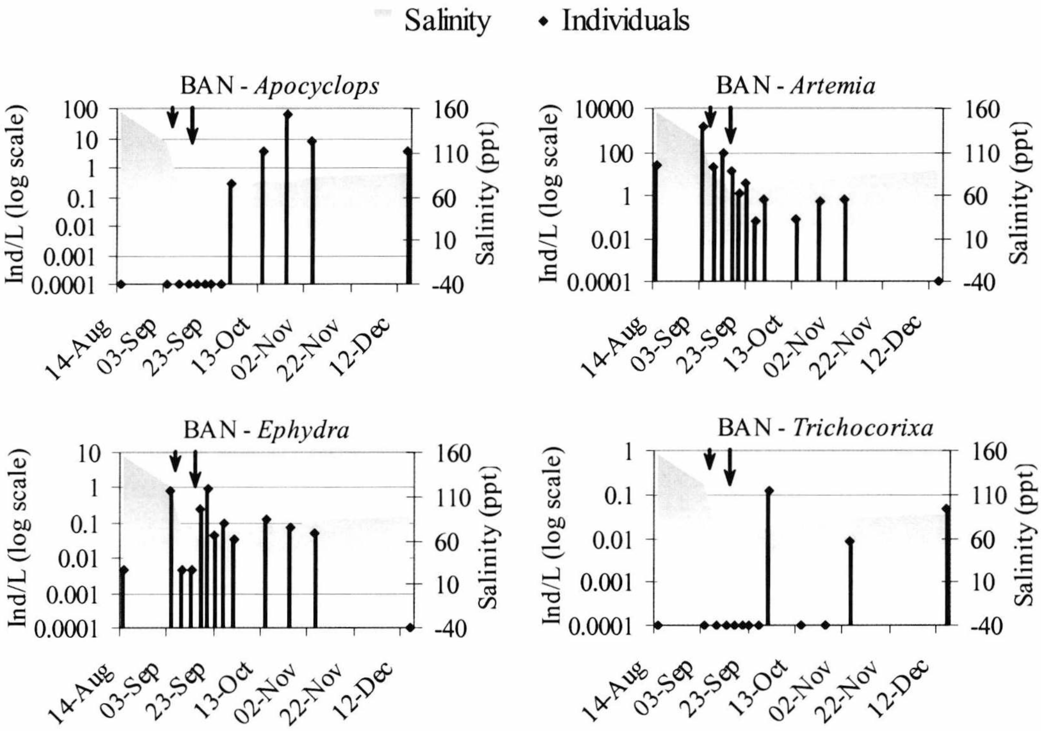


Figure 6.10 Biotic responses to Hurricanes Luis and Marilyn (BAN, 1995). Arrows indicate hurricane events.

The colour of the *Artemia* captured after the hurricanes gradually paled from red to nearly white. This colour change may have resulted from decreased haemoglobin concentration in response to increasing dissolved oxygen concentrations resulting from declining salinities (DeWachter *et al.* 1992; Spicer & El-Gamal 1999). On November 5th, *Artemia* were dragging long, thin green algal filaments that were attached to their legs. By the next sampling date, December 16th, *Artemia* were absent from the pond (Figure 6.10). Fouling of *Artemia's* swimming and feeding appendages may have contributed to their demise, as described by Kristensen & Hulsher-Emeis (1972).

Meanwhile, a transitional community had developed with the appearance of *Trichocorixa* and *Apocyclops* 2 weeks after the second hurricane (and nearly 4 weeks after the first hurricane). The timing of these appearances corresponded with development times of both species. Dexter (1993) showed that *A. dengizicus* requires at least 2 weeks to reach sexual maturity. The population of *A. panamensis* is likely to have developed from a stock of resistant eggs within BAN, while the *Trichocorixa* population was more likely initiated by colonization events. Balling & Resh (1984) showed that 90% of *T. reticulata* eggs hatch 12 to15 days after being deposited at the appropriate salinity. *Trichocorixa* eggs have not been shown to resist long periods of very high salinities as occurred in BAN before the hurricanes. It is therefore likely that *Trichocorixa* colonized from reservoir populations that existed in less saline pools nearby. The *Trichocorixa* population persisted at low densities in BAN throughout the remainder of 1995. Zero values for *Trichocorixa* during October (Figure 6.10) reflected a lack of specimens captured in plankton samples but their presence in the pond was confirmed visually (see Section 3.4 (a)). Unlike *Trichocorixa*, the *Apocyclops* population grew exponentially after first appearing. Exponential growth continued for one month with a resultant 100-fold increase in population density to a maximum of 62 ind/L (Figure 6.10). The *Apocyclops* population subsequently declined and then stabilized at 7 ind/L. These population dynamics (exponential growth followed by a decline to carrying capacity) fit the pattern of a colonizing species in an uncompetitive environment.

Turnover from a high-salinity fauna, consisting of *Artemia* and *Ephydra*, to a low-salinity fauna, consisting of *Apocyclops* and *Trichocorixa*, was completed in BAN 3 months after the hurricanes.

6.2 (f.*ii*) Hurricane Georges and subsequent rains, 1998

1998 was the rainiest year in the BVI for at least the previous 25 years (Rowan Roy and David Jones, pers. comm. 1998). As a result, none of the 4 ponds studied in 1998 supported communities comprised solely of high salinity species (*Artemia, Ephydra* and *Cletocamptus*) during the dry summer season before Hurricane Georges (Figure 6.11). BAN contained a mix of high- and low-salinity species, *Artemia*, *Cletocamptus* and *Trichocorixa,* in early August, 1998 (Figure 6.11(a)). Hurricane Georges, on September 22nd, 1998, diluted BAN from 83 to 64 ppt, crossing the threshold for a faunal turnover. Gradual decline in the *Artemia* population occurred over 4 weeks following the hurricane. The *Trichocorixa* population appeared unaffected, but *Cletocamptus* declined quickly (Figure 6.11(a)). As during the 1995 hurricanes, *Apocyclops* appeared within 2 weeks of the dilution event. *Apocyclops* increased exponentially for more than one week, after which it increased at a slower rate. The faunal turnover was complete within 6 weeks after the hurricane, when a lower-salinity community consisting of *Apocyclops* and *Trichocorixa* was present (Figure 6.11(a)).

Changes in species composition also occurred after Hurricane Georges in GUA, JOS and LON (Figure 6.11(b - d)). Samples collected just after Hurricane Georges in these ponds contained ciliates that swam sluggishly, and ciliate populations declined and/or disappeared soon after. Rotifers colonized GUA (Figure 6.11(b)) and LON (Figure 6.11(d)) within 2 weeks after the hurricane. Further dilution by heavy rains on October 21st killed both of these rotifer populations, and samples taken immediately after these rains contained hundreds of dead rotifers. A rotifer population was present in JOS before Hurricane Georges (Figure 6.11(c)). This population was greatly reduced by the dilution events, but it did not disappear until 8 days after the October 21st rains. These observations indicate that rotifers and ciliates were less able than arthropods to withstand abrupt osmotic changes in their environment.

Dasyhelea, which disappeared immediately after the hurricane in LON (Figure 6.11(d)), may also have been sensitive to abrupt salinity changes, but other factors, such as sediment disturbance by seawater inundation (see Section 4.2(a.*ii*)), were also likely to have disrupted the population of *Dasyhelea* in LON.

Apocyclops appeared in LON (Figure 6.11(d)) within a few days of Hurricane Georges. It may have been present in nearby mangrove pools from which it was washed into the pond during seawater inundation. *Apocyclops* became highly abundant within 10 days of the hurricane, after which it stabilized at a lower density. This pattern of rapid population growth was consistent with that seen in BAN after dilution events in 1995 and 1998 (Figure 6.10 and 6.11(a)).

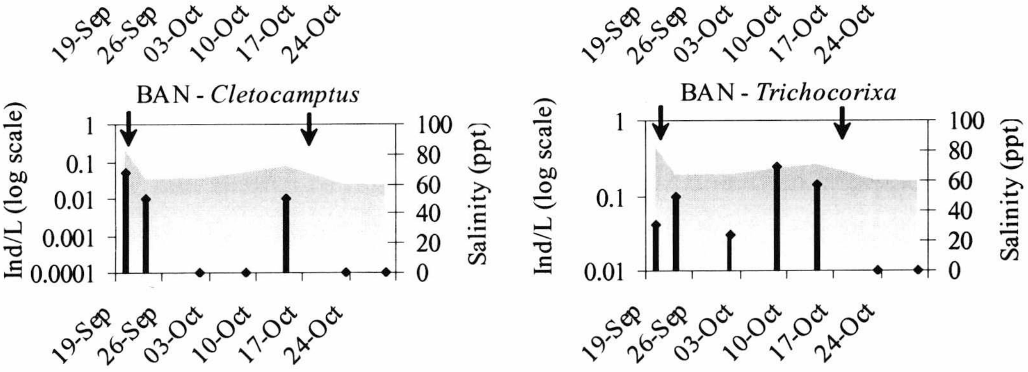


Figure 6.11 (a) Biotic responses to Hurricane Georges and subsequent rains in BAN, 1998. Rain storms are indicated by arrows.

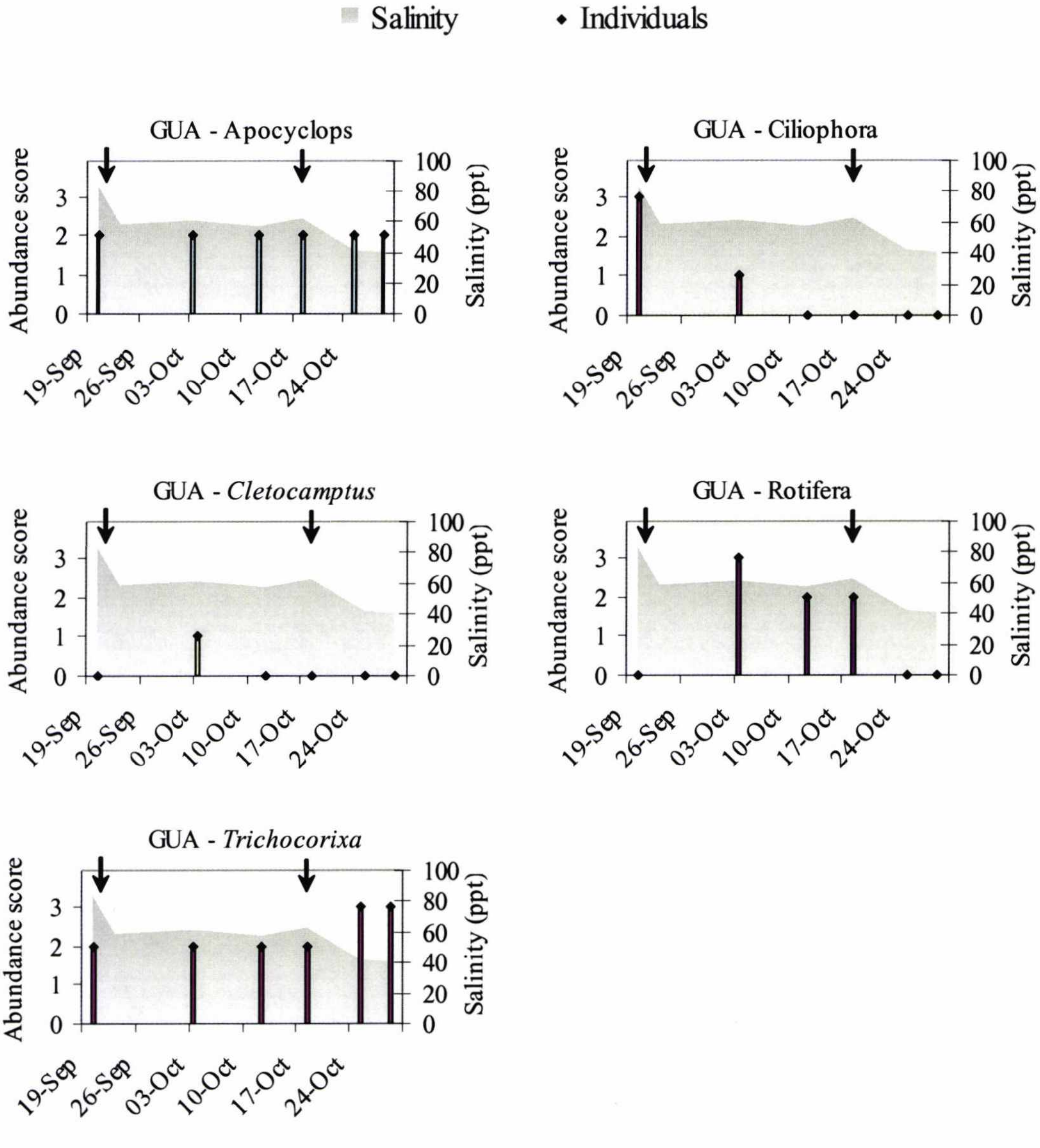


Figure 6.11 (b) Biotic responses to Hurricane Georges and subsequent rains GUA, 1998. Rain storms are indicated by arrows.

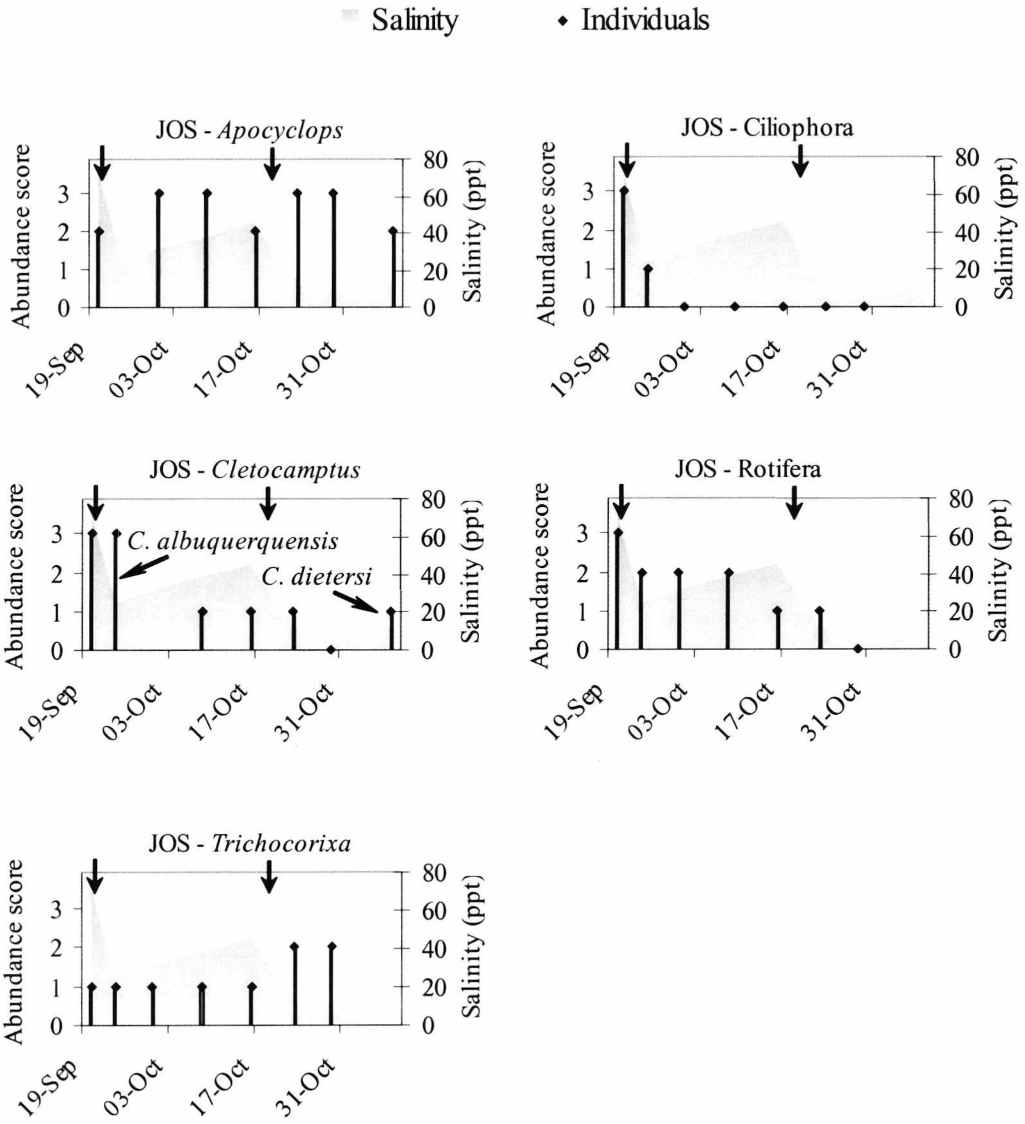


Figure 6.11 (c) Biotic responses to Hurricane Georges and subsequent rains in JOS, 1998. Rain storms are indicated by arrows.

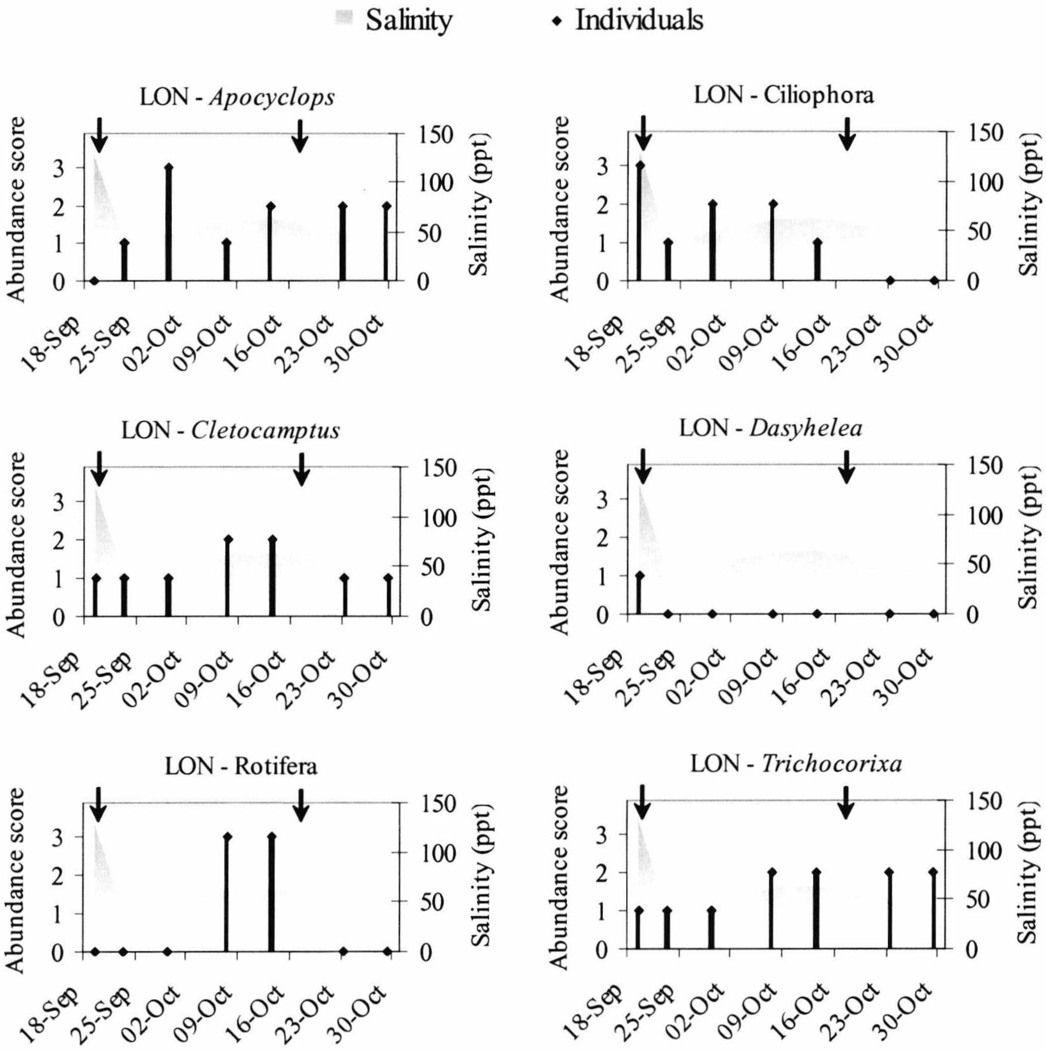


Figure 6.11 (d) Biotic responses to Hurricane Georges and subsequent rains LON, 1998. Rain storms are indicated by arrows.

Cletocamptus populations showed variable responses to Hurricane Georges and subsequent rains. They were not affected in GUA or LON, but they disappeared and later reappeared in BAN and JOS. The declining *Cletocamptus* population in JOS after the hurricane was subsequently identified as *C. albuquerquensis* (Figure 6.11(c)). This population died out approximately 6 weeks after the hurricane (8 days after the Oct 21st rains) and was replaced by *C. deitersi* shortly thereafter. *C. deitersi* was also present in LON 5 weeks after the hurricane, but it is not known which species was present in LON beforehand. It is interesting to apply these observations to an anomalous finding reported by both Greenwald & Hurlbert (1993) and Hart *et al.* (1998) in separate studies. These authors observed 2 abundance peaks for *Cletocamptus* in microcosm cultures from the Salton Sea and a coastal lagoon in San Diego, CA, respectively.

Greenwald & Hurlbert recorded an initial peak at 30 – 39 ppt and another peak at 65 ppt, while Hart *et al.* recorded one peak at 17 ppt and a second peak at 34 ppt. Hart *et al.* identified the species as *C. deitersi*, while Greenwald & Hurlbert did not name the species. Further inquiry into the population dynamics of these closely related copepods is necessary to determine their relationships with salinity and with one another.

6.2 (g) Biotic interactions

Biotic control of species composition was indicated by significant associations between taxa with overlapping salinity ranges (Table 6.5). A highly significant negative association was found between *Artemia* and ciliates. This association may be competitive or predatory. The former may be more likely as both *Artemia* and ciliates filter phytoplankton, and the planktonic ciliates found in BVI salt ponds were larger than the size range (3 to 50 μm diameter, Persoone & Sorgeloos 1980) of particles normally taken by *Artemia.* Competitive exclusion of *Artemia* by small filter-feeding zooplankton, such as rotifers, crustaceans and ciliates, has been previously suggested by Kristensen & Hulsher-Emeis (1972) and by Persoone & Sorgeloos (1980). However, Hart *et al.* (1998) showed that protists, which normally dominated the plankton in Salton Sea microcosms, disappeared when *Artemia* was abundant. Further study will be necessary to determine the mechanism by which one excludes the other.

Artemia was also negatively associated with *Apocyclops* (Table 6.5). *Apocyclops* is a successful predator despite its tiny size, and members of this genus have been shown to prey on *Artemia* and other invertebrates in laboratory microcosms (Dexter 1993; Hammer 1986; Hammer & Hurlbert 1992; Hart *et al.* 1998). Groups of 5 – 6 cyclopoid copepods have been reported to attack and dismember *Artemia* (Kristensen & Hulsher-Emeis 1972). The relationship between *Apocyclops* and *Artemia* observed here is therefore likely to be that of predator and prey. When a new population of *Apocyclops* developed in a BVI pond containing an *Artemia* population, *Artemia* usually disappeared within one month (see Figures 6.6(a, c, d & e), 6.10 and 6.11(a)). In cases where the *Apocyclops* population did not survive, however, the *Artemia* population remained (Figure 6.6 (a. b & e)).

Table 6.5 Significance levels of associations between species pairs. Values indicate significance levels for tests of pairs of species using a 2-sided Pearson Chi-Square test with 3 degrees of freedom.

	Apocyclops	*Cletocamptus*	*Trichocorixa*	*Ciliophora*
Pisces	0.000 (+)	0.500	0.610	0.348
Artemia	0.018 (-)	0.536	0.298	0.000 (-)
Apocyclops		0.100	0.146	0.016 (+)
Cletocamptus			0.362	0.039 (+)
Trichocorixa				0.073

Positive associations occurred between ciliates and *Apocyclops* and between ciliates and *Cletocamptus* (Table 6.5). The nature of these relationships is unclear, but copepods may have been controlling a predator or a food competitor, such as *Artemia* and rotifers. Hart *et al.* (1998) reported that rotifer populations in microcosm cultures from the Salton Sea were reduced by predation from *Apocyclops dengizicus. Cletocamptus* has been reported to consume the eggs of planktonic invertebrates and prevent their colonization in microcosms (Hammer & Hurlbert 1992).

Similarly, a highly significant positive association was found between fish and *Apocyclops* (Table 6.5). This may have been due to the elimination of larger invertebrates by fish, which are major predators of macroinvertebrates in saline ponds (Hurlbert *et al.* 1986; Kristensen & Hulsher-Emeis 1972; Lonzarich & Smith 1997). Soto & Hurlbert (1991) also noted that the presence of fish, while drastically reducing populations of other invertebrates, did not effect cyclopoid populations. The removal of planktonic grazers by fish may have released *Apocyclops* nauplii, which are herbivorous, from competition and so boosted *Apocyclops* populations. An association between fish and *Artemia* could not be assessed because the overlap in salinity range and distribution was too narrow to provide sufficient data.

No significant association was found between the presence and absence of *Trichocorixa* and that of any other common water-column organism (Table 6.5). Nevertheless, *Trichocorixa* was conspicuously less abundant in ponds that contained fish (e.g. BON and WB, Table 6.3) than in ponds that rarely or never contained fish (e.g. GUA and JOS).

This chapter described the composition of salt pond communities and population dynamics of their fauna, with the exception of birds. The diversity and abundance of birds at salt ponds is discussed in the next chapter.

Chapter 7: Abundance and Distribution of Birds

7.1 Introduction

Waterbirds are highly dependent upon wetland habitats, and migratory species depend on extensive, cross-national networks of wetlands. The extent to which waterbirds use hypersaline wetlands, in particular, is not well known, but a few studies have shown that hypersaline water bodies represent critical habitats for waterbird populations. Britton & Johnson (1987), for example, recorded 200 species of birds from the saline lakes of Camargue, France. Tanner *et al.* (1999) reported that the hypersaline Salton Sea in central California is used by more shorebirds during late summer than any other habitat. Kingsford & Porter (1994) showed that an Australian salt lake had 10 times more waterbirds than an adjacent freshwater lake only 3 km away. Warnock & Takekawa (1995) showed that salt pond levees were the most important habitat for Western Sandpipers in the San Francisco Bay estuary, and Takekawa *et al.* (2001) showed that benthivorous waterbird populations were 4 times as dense in salt ponds than in baylands during winter and spring. These authors attributed this preference for hypersaline water bodies over freshwater or estuarine water bodies to a greater abundance of appropriate food resources in hypersaline systems.

This chapter describes the abundance and diversity of waterbirds in BVI salt ponds. The data presented here are intended to provide baseline information about avian use of salt pond habitats, and they will be valuable to environmental organizations in arguing for the conservation of these habitats in the BVI.

7.2 Results and Discussion

7.2 (a) Avian use of salt ponds

A total of 45 species of birds were recorded from salt ponds between 1995 and 2001 (Table 7.1). Twenty-three species of shorebirds, 4 species of waterfowl, 8 herons and egrets, and the Greater Flamingo were represented in addition to 3 species of forest birds, one kingfisher, and 4 seabirds.

Table 7.1 Bird species recorded from BVI salt ponds between 1995 and 2001, with occurrence frequencies for each species counted in the 1995 monthly surveys

Common name	Scientific name	Frequency of occurrence in bird counts (N = 107)
Herons/egrets		
Cattle Egret	*Bubulcus ibis*	*
Great Blue Heron	*Ardea herodias*	5%
Great Egret	*Casmerodius albus*	*
Green-backed Heron	*Butorides striatus*	6%
Little Blue Heron	*Egretta caerulea*	13%
Snowy Egret	*Egretta thula*	2%
Tricolored Heron	*Egretta tricolor*	<1%
Yellow-crowned Night Heron	*Nycticorax violaceus*	3%
Shorebirds		
Black-bellied Plover	*Pluvialis squatarola*	15%
Black-necked Stilt	*Himantopus mexicanus*	64%
Clapper Rail	*Rallus longirostris*	*
Common Snipe	*Gallinago gallinago*	*
Dowitcher	*Limnodromus sp.*	11%
Greater Flamingo	*Phoenicopterus ruber ruber*	23%
Greater Yellowlegs	*Tringa melanoleuca*	27%
Killdeer	*Charadrius vociferus*	<1%
Least Sandpiper	*Calidris minutilla*	<1%
Lesser Yellowlegs	*Tringa flavipes*	48%
Phalarope	*Phalaropus tricolor*	*
Ruddy Turnstone	*Arenaria interpres*	29%
Sanderling	*Calidris alba*	*
Semipalmated Plover	*Charadrius semipalmatus*	40%
Semipalmated Sandpiper	*Calidris pusilla*	26%
Snowy Plover	*Charadrius alexandrinus*	10%
Solitary Sandpiper	*Tringa solitaria*	*
Spotted Sandpiper	*Actitis macularia*	28%
Stilt Sandpiper	*Calidris himantopus*	<1%
Western Sandpiper	*Calidris mauri*	3%
Whimbrel	*Numenius phaeopus*	4%
White-rumped Sandpiper	*Calidris fuscicollis*	*
Willet	*Catoptrophorus semipalmatus*	9%
Wilson's Plover	*Charadrius wilsonia*	48%
Waterfowl		
American Coot	*Fulica americana*	<1%
Blue-winged Teal	*Anas discors*	5%
Common Moorhen	*Gallinula chloropus*	<1%
White-cheeked Pintail	*Anas bahamensis*	41%

* Not counted in the 1995 survey

Table 7.1 (continued) Bird species recorded from BVI salt ponds between 1995 and 2001, with occurrence frequencies for each species counted in the 1995 monthly surveys.

Common name	Scientific name	Frequency of occurrence in bird counts (N = 107)
Seabirds & Hawks		
Brown Pelican	Pelecanus occidentalis	*
Laughing Gull	*Larus atricilla*	*
Least Tern	*Sterna antillarum*	*
Magnificent Frigate	*Fregata magnificens*	*
Osprey	*Pandion haliaetus*	*
Roseate Tern	*Sterna dougallii*	*
Forest birds & Kingfishers		
Belted Kingfisher	*Ceryle alcyon*	*
Cliff Swallow	*Hirundo pyrrhonota*	*
Mangrove Cuckoo	*Coccyzus minor*	*
Yellow Warbler	*Dendroica petechia*	*

* Seabirds and forest birds were not included in monthly counts.

The most common species were White-cheeked Pintail ducks (*Anas bahamensis*), Semipalmated Plovers (*Charadrius semipalmatus*), Wilson's Plovers (*Charadrius wilsonia*), Black-necked Stilts (*Himantopus mexicanus*), and Lesser Yellowlegs (*Tringa flavipes*), each occurring in at least 40% of bird counts (Table 7.1). These species were also the most abundant in ponds (Figure 7.1). Eighty-one percent of all birds counted during 1995 belonged to this group of species.

Spotted Sandpipers (*Actitis macularia*), Ruddy Turnstones (*Arenaria interpres*) Semipalmated Sandpipers (*Calidris pusilla*), Greater Flamingos (*Phoenicopterus ruber ruber*) and Greater Yellowlegs (*Tringa melanoleuca*) were also common, each occurring in more than 20% but less than 40% of bird counts (Table 7.1). The current Greater Flamingo population was reintroduced to salt ponds of the BVI in 1991, 50 years after they were extirpated from the Virgin Islands (Lazell 2002). An initial flock of 18 flamingos nested successfully on Anegada for the first time in 1995, after being joined by 4 wild flamingos. This population has continued to nest annually in the Anegada ponds, and their population has grown to 84 as of 2002. A much smaller flock of 6 flamingos in GUA has not reproduced.

Laughing Gulls (*Larus atricilla*), Roseate Terns (*Sterna dougallii*) and Least Terns (*Sterna antillarum*) nested on the sand spits and islands within the Anegada salt ponds during May and June of 1995, 1999 and 2000 and probably also other years when these ponds were not checked. Flocks of Laughing Gulls and Least Terns were also seen in JOS and BEL during April of 2000. Scott & Carbonell (1986) reported Least Terns breeding at salt ponds in the Bahamas, the Dominican Republic, Jamaica, the Netherlands Antilles, and Puerto Rico. Roseate Terns and Least Terns are globally endangered species (http://ecos.fws.gov), and salt ponds of the Caribbean therefore represent a critical resource for the survival of these species.

Magnificent Frigates (*Fregata magnificens*) and Osprey (*Pandion haliaetus*) were occasionally observed hunting over ponds. Flocks of migrating Cliff Swallows (*Hirundo pyrrhonota*) hunted insects over salt ponds, as did fishing bats (*Noctilio leporinus*) at night.

The Mangrove Cuckoo (*Coccyzus minor*) and the Yellow Warbler (*Dendroica petechia*) nested in mangrove forests fringing salt ponds. Yellow Warblers are extremely sensitive to habitat disruption (Kathiresan & Bingham 2001; Mayer & Chipley 1992). Removal of about 1500 m^2 of fringing mangrove forest from Guana's salt pond in 1980 resulted in the disappearance of Yellow Warblers from Guana Island (Mayer & Chipley 1992), and this species has not recolonized despite regrowth of mangroves.

7.2 (b) Temporal variation in bird abundance

Mean abundance of birds in salt ponds was greatest in February (59 ± 91 birds/pond) and March (124 ± 136 birds/pond) and again in September (49 ± 57 birds/pond). May and June showed the lowest bird abundance, when mean counts for the 10 ponds dropped below 20 birds (Figure 7.1). The seasonal peaks in bird abundance reflected the arrival of migratory waterbirds.

Only White-cheeked Pintails, Wilson's Plovers, Black-necked Stilts and Flamingos were recorded during every month of 1995 (Figure 7.1). Migratory populations augmented resident populations in the winter so that White-cheeked Pintails, Semipalmated Plovers, Black-necked Stilts and Lesser Yellowlegs were most abundant from January through March. The populations of Wilson's Plovers, in contrast, were relatively stable throughout 1995.

Several less common species were also migratory, appearing in the BVI mainly during winter months (see "other species", Figure 7.1). These included Spotted Sandpipers, which were most abundant in December, Ruddy Turnstones, which were most abundant in March, and Greater Yellowlegs, which were most abundant in March and October.

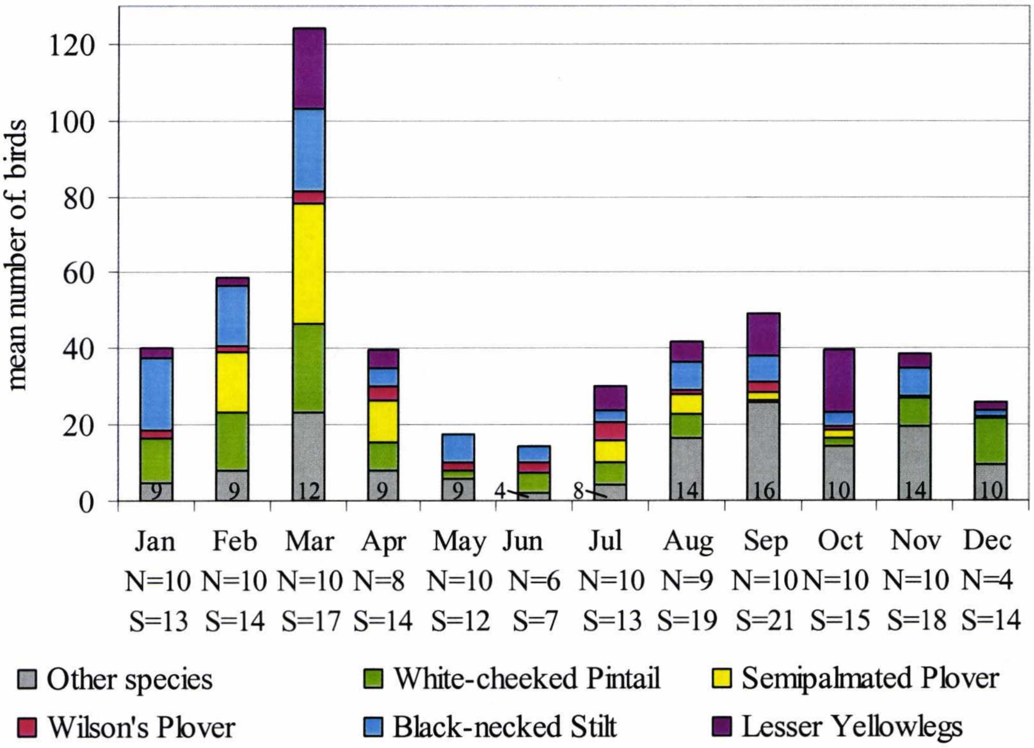


Figure 7.1 Monthly abundances of common birds during 1995. N indicates the total number of ponds sampled, and S indicates the total number of species counted.

7.2 (c) Species distributions among ponds

Table 7.2 shows mean bird abundance, maximum counts and species richness in each pond during 1995. Mean abundance was greatest in BEL, FLA, PTP and BAN. The highest total bird count (361 birds) occurred in BEL, followed by high bird counts in FLA (319 birds) and PTP (238 birds). The lowest average abundance was in SAL, where birds, totalling 9 individuals for the year, were seen on only 3 of 11 visits. Mean bird abundance in other ponds ranged between 24 and 34. The total number of species, excluding sea and land birds, recorded in each pond over the entire year varied from 8 to 21 and averaged 15 (Table 7.2).

Species richness (the total number of species recorded) was greatest in JOS and WB, with 21 and 20 species, respectively, and it was lowest in PTP and SAL, with 11 and 8 species, respectively. Momentary species richness (the mean number of species recorded on a single visit) was always lower than long-term species richness (Table 7.2). Low momentary species richness as compared with long-term species richness reflects the frequent movement of birds into and out of ponds.

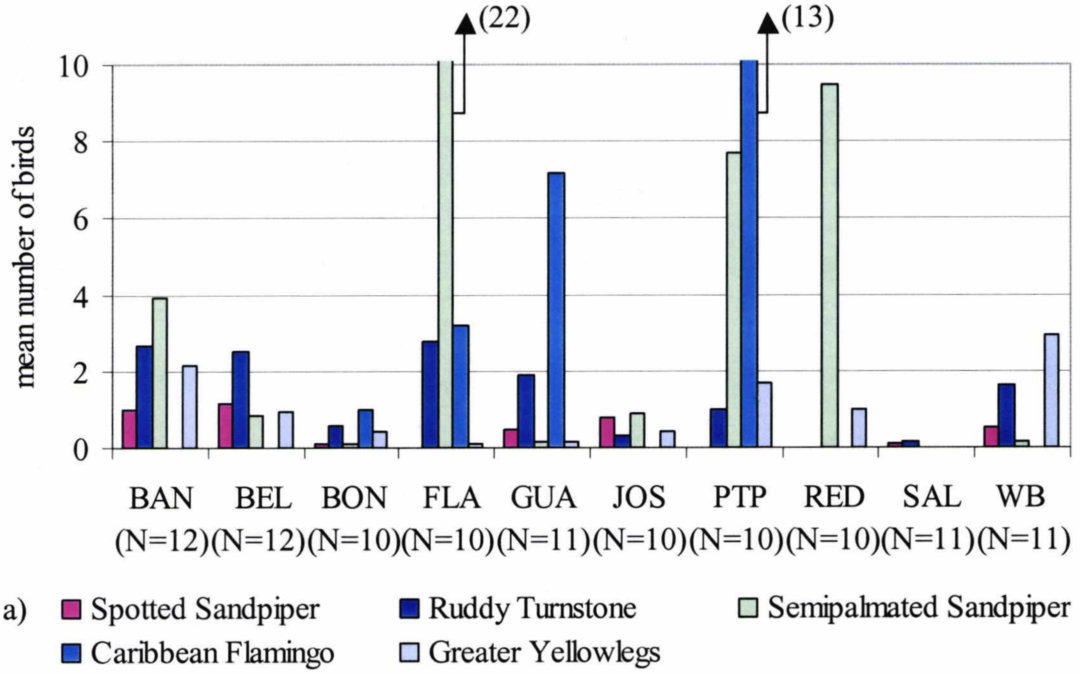
The Snowy Plover was the only species showing a restricted distribution pattern, occurring only on Anegada. Scott & Carbonell (1986) similarly described a restricted distribution of Snowy Plovers in Puerto Rico, where their only breeding site was the Cabo Rojo salt ponds. All other species observed in the present study occurred on multiple islands within the BVI, but they were neither distributed evenly across ponds nor did all species share the same pattern of distribution among ponds (Figure 7.2). This finding suggests that birds generally showed preferences for certain pond characteristics rather than for particular islands.

Shoreline characteristics, such as the existence of open sand flats, may have affected habitat choice by some species. Semipalmated Sandpipers were far more abundant in FLA, PTP and RED (mean counts 22 ± 43, 7.7 ± 18 and 9.5 ± 27, respectively) than in other ponds (mean counts ranged from 0 in SAL to 3.9 ± 5.7 in BAN, Figure 7.2(a)). Large sand spits, sand islands, and sparsely vegetated flats were particular to the ponds preferred by Semipalmated Sandpipers. Though it may be argued that the distribution of these sandpipers illustrated a preference for the island of Anegada rather than for particular pond characteristics, the species' near absence (one individual seen during 1995) in BON, an Anegada pond with a well-forested shoreline and few sand flats, indicates a clear preference for ponds with open sand flats even within Anegada.

Table 7.2 Bird abundance and species richness in 10 ponds during 1995

Pond	Location	Counts (N)	Mean bird count	Maximum bird count	Species richness	Mean momentary species richness*
BAN	Beef Island	12	44 ± 39	129 (Oct)	16	5.2 ± 2.4
BEL	Tortola	12	94 ± 131	361 (Mar)	15	4.8 ± 2.0
BON	Anegada	10	27 ± 50	146 (Mar)	15	2.7 ± 2.3
FLA	Anegada	10	85 ± 93	319 (Mar)	15	4.7 ± 2.3
GUA	Guana	11	34 ± 14	57 (Apr)	14	6.8 ± 1.9
JOS	Tortola	10	24 ± 23	67 (Dec)	21	5.0 ± 3.2
PTP	Anegada	10	87 ± 81	238 (Mar)	11	6.2 ± 2.6
RED	Anegada	10	29 ± 40	124 (Sep)	14	3.4 ± 2.7
SAL	Salt Island	11	1 ± 2	2 (Aug)	8	0.81 ± 1.6
WB	Tortola	11	27 ± 27	95 (Mar)	20	5.9 ± 2.4

* Mean number of species present in each bird count.



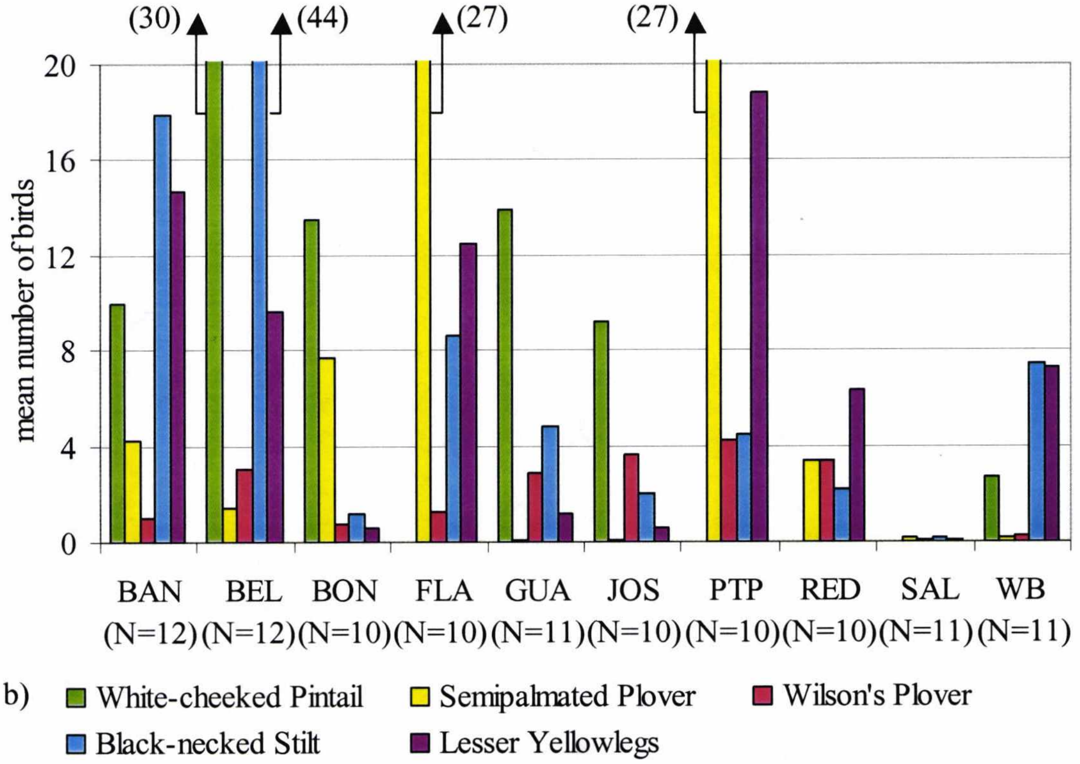


Figure 7.2 Differences in the abundance of avian species among ponds during1995

White-cheeked Pintails, conversely, were absent from the same ponds in which Semipalmated Sandpipers were most abundant. Pintails appeared to prefer ponds with well-vegetated shorelines such as BAN, BEL, BON, GUA and JOS (Figure 7.2(b)). Abundance of this species in WB was probably underestimated because of the difficulties in seeing ducks behind mangrove islands and in channels. Norton *et al.*

(1986) showed that White-cheeked Pintails in the U.S. Virgin Islands preferred small ponds with salinities near 20 ppt. White-cheeked Pintails were recorded in ponds of much higher salinities during this study. Their abundance in BEL between January and March 1995, for example, averaged 115 ± 22 birds when salinities averaged 154 ± 21ppt. They also appeared to have no clear preference for small ponds, being most abundant at BEL, the largest pond outside of Anegada.

Other species also showed greater abundance in particular ponds. These species included Semipalmated Plovers, which were most abundant at FLA and PTP, Spotted Sandpipers, which were most abundant in FLA, GUA and PTP, Black-necked Stilts, which were most abundant in BAN and BEL, and Lesser Yellowlegs, which were most abundant in BAN, BEL, FLA and PTP (Figure 7.2). These findings suggest that birds were choosing specific habitat characteristics at salt ponds. Ponds in the BVI varied in several characteristics that may have been important to shorebirds, including size, shoreline morphology and vegetation, salinity and degree of human encroachment. Because bird counts in this study were neither regular nor standardized to time of day (see Section 3.4 (g)), it was not possible to make statistical comparisons of bird populations with specific pond characteristics.

7.2 (d) Choice and availability of prey

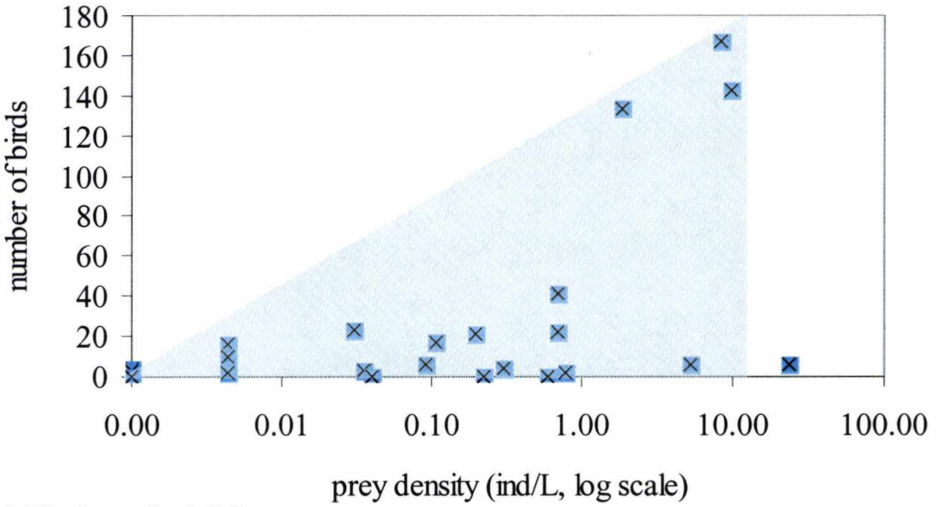
It is generally thought that birds choose habitats with abundant food (e.g. Kathiresan & Bingham 2001; Kingsford & Porter 1994). This has been shown for 2 species of stilts (Cullen 1994; Pierce 1986), for White-cheeked Pintails (Norton *et al.* 1986) and for Greater Flamingos (Arengo & Balsdassarre 1998; Hurlbert *et al.* 1986). However, other authors have indicated that food abundance estimates are imperfect indicators of food availability (Arengo & Baldassarre 1999; Hurlbert *et al.* 1986), and other factors, such as water level (Comin *et al.* 1999) may strongly affect habitat choices.

Observations of feeding behaviours in BVI ponds indicated that Black-necked Stilts and Lesser Yellowlegs fed in shallow water, apparently pecking macroinvertebrates from the water column and benthos of ponds. Potential food items included *Trichocorixa, Artemia, Ephydra* and *Dasyhelea*. Cullen (1994) showed that Black-necked Stilts subsisted almost entirely on *Trichocorixa* in Puerto Rico, and their diet was likely to be similar in the BVI. Fly larvae are major prey items for waders in general (Herbst 1990; Rehfisch 1994).

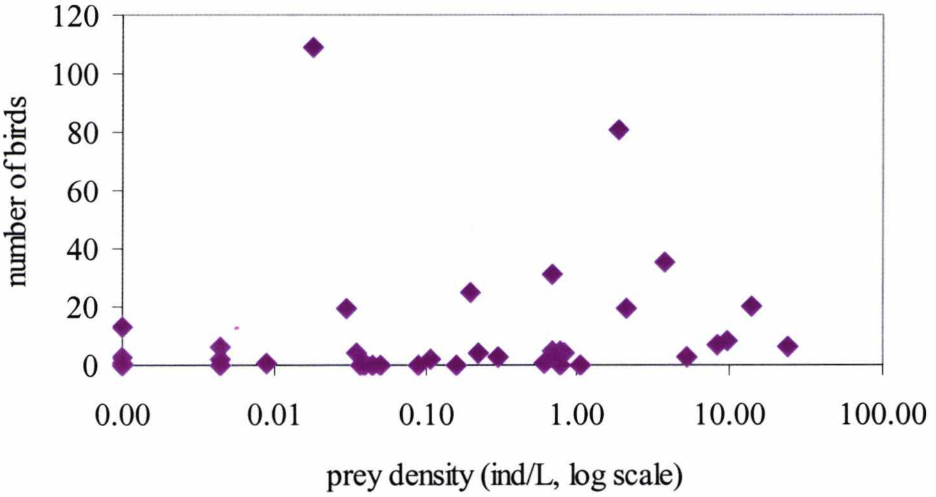
Semipalmated Plovers and Semipalmated Sandpipers fed by running and pecking at the ground along the water's edge, and they may have been catching small insects (e.g. emergent fly larvae). White-cheeked Pintails fed in deeper water by inverting themselves, apparently dabbling in the bottom sediments. Norton *et al.* (1986) showed that White-cheeked pintails in the Virgin Islands feed primarily on algae, *Ruppia*, corixids, insect larvae and snails. Wilson's Plovers preyed on fiddler crabs (*Uca burgersi*), and detached crab claws were often scattered across pond shores at which both Wilson's Plovers and fiddler crabs were abundant, such as GUA and JOS. Hockey & Barnes (1997) reported that fiddler crabs are eaten extensively by waders and are especially important in the diets of plovers.

Greater Flamingos were usually seen performing characteristic plankton-filtering behaviours (Rooth 1976) in GUA when either *Trichocorixa* or *Artemia* were present. Flamingos, however, are generalists and are not limited to filtering plankton (Olgive & Olgive 1986; Rooth 1965). When aquatic invertebrates were scarce, flamingos tended use their bills to shovel mud towards their feet while turning in circles, probably seeking infaunal invertebrates or consuming mud. This behaviour left small pyramids of mud within ponds, as previously described by Jenkin (1957). On Anegada, flamingos were most often seen feeding in areas that contained benthic fly larvae, and their sweeping bill tracks were apparent in the sediments. Fly larvae are known to comprise the bulk of flamingo diets in the Yucatan (Arengo & Baldassarre 1998).

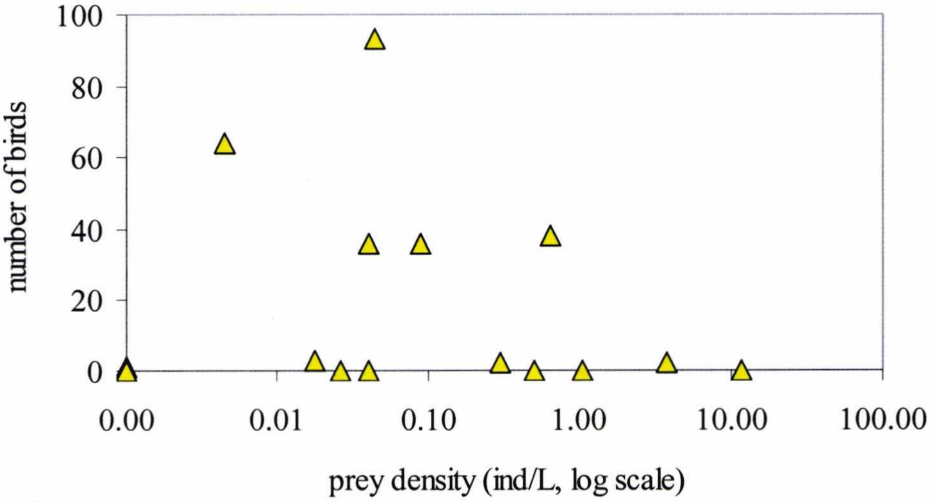
Potential invertebrate prey reached high densities in BVI ponds, but their populations fluctuated both temporally and spatially in response to salinity fluctuations (see Section 6.2(d)). It was expected that birds faced with declining prey populations would either switch their diet (e.g. Pierce 1985) or fly to another pond. Birds were regularly seen flying between ponds. Graphical representation of the relationship between bird abundance and overall prey abundance showed a general positive trend (as evidenced by a triangular-shaped distribution of points) for Black-necked Stilts and White-cheeked Pintails, but a clear trend was not identifiable for Semipalmated Plovers and Lesser Yellowlegs (Figure 7.3).



a) Black-necked Stilt

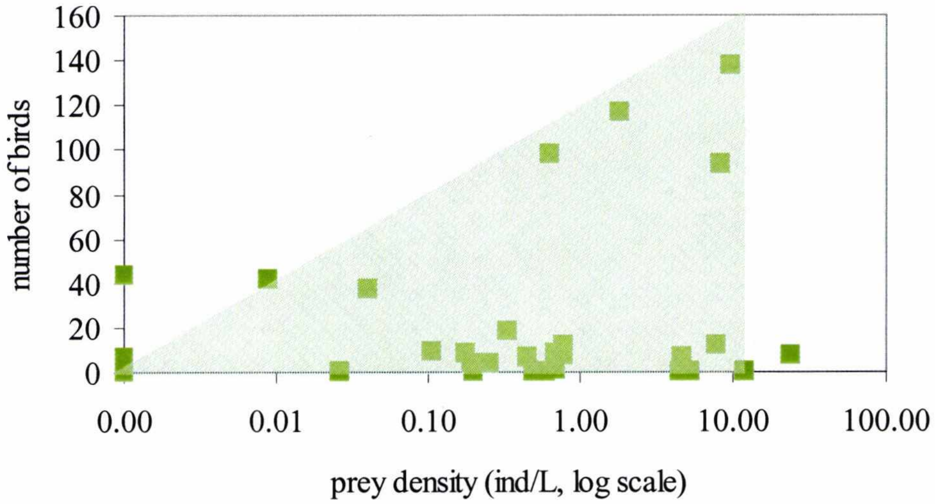


b) Lesser Yellowlegs



c) Semipalmated Plover

Figure 7.3 Scatter plot of bird abundance versus prey density. A triangular shaded area indicates a positive relationship between bird abundance and prey density.



d) White-cheeked Pintail

Figure 7.3 (continued) Scatter plot of bird abundance versus prey density. A triangular shaded area indicates a positive relationship between bird abundance and prey density.

Future studies should identify stronger relationships between bird abundance and pond characteristics than was possible in this preliminary study. Ringing (leg banding), in particular, could be used to track movements of birds between ponds and directly compare these movements with prey abundance, vegetation cover, salinity, and other habitat characteristics. However, the BVI government currently discourages ringing (Bertrand Lettsome, pers. comm. 2000). The value of further study focussing on habitat choice by birds at salt ponds is indicated by the distribution patterns identified in this survey.

This chapter evaluated the use of salt ponds by resident and migratory bird populations and concludes the presentation of new data in this thesis. The following chapter compiles a variety of the data so far presented into a classification system for salt pond habitats.

Chapter 8: Ecological Classification of Salt Ponds

8.1 Introduction

An ecosystem classification permits general predictions about habitats and their communities by measuring a limited number of variables, and it provides a model upon which further investigations can be based. However, the diversity of hypersaline water bodies makes them difficult to classify (Moss 1994). The greatest challenge in creating a successful classification scheme is to identify the most appropriate variables for distinguishing habitat types. Existing classification systems, described below, are each based on one variable that identifies the salinity, hydrology, or geology of hypersaline water bodies.

Hammer (1986) used salinity to classify saline lakes as hyposaline (3 – 20 ppt), mesosaline (20 – 50 ppt) or hypersaline (>50 ppt). Carpelan (1957) also used salinity to differentiate between hypersaline waters (40 to 70 ppt) and brine (>70 ppt). Por (1985) classified coastal salt ponds into 3 salinity categories: polyhaline-euhaline (≤37 ppt), metahaline (38 – 70 ppt) and hypersaline (>70 ppt). The category definitions used by these authors are inconsistent with one another, and they make the term "hypersaline" ambiguous. Barbe et al. (1990), recognizing that the term hypersaline represents a diversity of environments, classified high-salinity ponds as calcite, gypsum, or halite ponds, depending on which salt was most often deposited.

All of these classification systems imply that pond salinities are relatively stable, but, in many cases, both inland lakes and coastal salt ponds experience large seasonal variations in salinity. As a result, a single water body might be placed in one of several salinity classes depending on when the salinity measurement is made (Lieffers & Shay 1983).

Williams (1998) used hydrology to differentiate inland salt lakes by their inundation period, distinguishing among permanent salt lakes, which never dry, intermittent salt lakes, which dry seasonally, and episodic salt lakes, which fill unpredictably and for short periods. These classes of salt lakes were both geographically separated and determined by climate. Gunter (1967), also using a hydrological variable, classified high-salinity coastal areas by their degree of connection with the sea. He differentiated between lagoons, pools and shore ponds intermittently connected with the sea and salt flats that were only inundated at the highest tides and otherwise remained dry. Por (1985) demonstrated the importance of hydrology in his definition of 'anchialine' pools, which required permanent subterranean connection with the sea, tidal fluctuations, and no permanent flow of freshwater from land.

Geology is often used to differentiate between athalassic saline water bodies, which are not of marine origin and almost always occur inland, and thalassic saline water bodies, which are of marine origin but are not necessarily coastal (e.g. Bayly 1972; McKenzie 1981; Persoone & Sorgeloos 1980). McKenzie (1981) elaborated upon the classification of thalassic lakes (to which all BVI salt ponds belong) by using biological characteristics to split this group into euthalassogenic saline lakes, in which the fauna is predominantly marine-derived, and metathalassogenic saline lakes, in which the fauna is predominantly freshwater-derived. BVI ponds, however, support a combination of freshwater-derived and marine-derived fauna (see Section 6.2(a.ii)).

Existing classification systems, which are based on single variables, may be inadequate to describe the variation among BVI salt ponds. Bacon (1994) emphasized the need to consider a complex of variables when modelling responses to sea level rise in Caribbean mangroves, and this argument applies equally to a classification model. In this chapter, a combination of chemical, hydrological, and biological variables are considered to produce a classification system for BVI salt ponds.

8.2 Methods

8.2 (a) Selection of variables

The entire data set produced by this study was codified to develop a system for ecological classification of salt ponds. Much consideration was given to the selection of classification parameters. Each variable monitored during this study was evaluated using the following requirements: it should be characteristic of the ecosystem; its variance among ecosystem subsets should be greater than within; it should describe a unique quality of the system (redundant variables were not accepted); and its measurement should be simple and rapid.

The following 21 variables were initially considered for inclusion:

Biological variables:

(1) dominant invertebrate group (Artemia-Ephydra or Trichocorixa-Copepoda),

(2) benthic producer community (BMC) (blue-black BMC, green BMC, Ruppia maritima (wigeongrass), or none; see Figure 6.3),

(3) tree density in the fringing mangrove forest (# trees/ha.; see Appendix D),

(4-7) percent of a pond's fringing forest represented by each of the 4 mangrove species (one variable for each species; see Table 4.3),

(8) presence/absence of red mangrove, Rhizophora mangle, patches (where red mangrove represented at least 75% of mangroves within a 500 m^2 or greater area, as described in Section 3.2 (h); see Table 4.3).

Physical/hydrological variables (see Table 4.1):

(9) pond area,

(10) location (designated by island),

(11) distance to the sea (closest point),

(12) sea connection/tidal influence (also see Table 4.2),

(13) bottom sediment type,

(14) inundation period.

Chemical variables (see Tables 5.1 and 5.3):

(15) annual salinity mean,

(16) annual salinity variance,

(17) mean dissolved oxygen,

(18) mean temperature,

(19-21) mean nutrient concentrations (NO_3, NH_4, and PO_4^{3-} = 3 variables).

Variable 1, dominant invertebrate group, was removed because its variance within ponds was as great as that between ponds. Variables 4 – 7, the 4 variables describing percent cover for each mangrove species, were combined into one variable that identified only the dominant mangrove at each pond. Variable 8, patches of R. mangle, was removed because it was highly correlated (hence redundant) with tidal influence (see Section 4.2 (d.iv)), which is included in variable 12. Variables 9, 10 and 11—pond area, location, and distance to the sea—were removed because they did not appear to be reliable indicators of ecosystem or hydrological dynamics (see Chapter 4). Variable 15, mean salinity, was left in the analysis, despite being highly variable within ponds and requiring multiple measurements, because salinity has been considered an important variable for defining variation among ponds in other studies (see Section 8.1). Variable 16, salinity variance, was removed because it requires many regular measurements and data were insufficient to include more than 10 ponds in the classification analysis. Variables 17 and 18, dissolved oxygen and temperature, were removed because they exhibited high diurnal variation and little consistent variation among ponds. Variables 19 – 21, nutrient concentrations, were removed because nutrient measurements are difficult and variability within ponds was similar to that between ponds.

8.2 (b) Definition of variables

Seven variables remained, but some were categorical while others were quantitative. Categorical variables were assigned scores to represent character states. These scores were ordered to reflect increasing connection with the sea; lower scores corresponded with greater isolation from the influence of seawater. Quantitative variables were categorized in order to normalize variances and means among all variables. This categorization also simplified the data matrix and was therefore preferred to z score transformations. Category limits were set at natural breaks in the data, and these breaks were identified by graphical analysis. The number of categories assigned to each variable depended on the number of natural breaks for continuous variables.

Category definitions and score values were assigned as follows (also see Table 8.1):

- Inundation period:
  2 : Pond inundated for less than 6 months per year
  3 : Pond inundated for more than 6 months per year
  4 : Pond permanently inundated
- Tidal influence/seawater inflow:
  0 : Pond with no direct connection to the sea and no tidal water movements
  1 : Pond with no visible connection to the sea, but tidal water movements were detected
  2 : Pond seasonally flooded with seawater through overland channels during high flood tides
  3 : Pond with visible 'seep'—constant trickle of seawater that originates from the ground above the pond water level
  4 : Pond permanently connected to the sea through visible, aboveground channels
- Mean salinity:
  1 : less than 60 ppt
  2 : 61 ppt to 90 ppt
  3 : 91 ppt to 120 ppt
  4 : greater than 120 ppt

  Note: There were few salinity data for ponds with short inundation periods (LEE, NOR, SAN, and HAN), but these ponds were all assigned to the first salinity category, as recorded salinities never exceeded 40 ppt in any of these ponds.

- Sediment type:
  - 1 : Sandy-mud sediments (substrate relatively firm, grey-brown and contained sand)
  - 2 : Mosaic of sandy-mud sediments in some areas and organic muck in other areas
  - 3 : Organic muck (thick layer of loose, black, organic sediments)
  - 4 : Gypsum/calcite crust (hard crust composed of precipitated salts)
- Benthic producer:

  Ponds were assigned to the following categories based on the most common type of photosynthetic community, which covered at least 30% of the benthos when present.
  - 0 : None or less than 30% of any other benthic producer category
  - 1 : Ruppia maritima
  - 2 : Green microbial mat
  - 3 : Blue-black microbial mat and/or red floc
- Mangrove density:
  - 2 : Less than 6,000 trees/ha.
  - 3 : More than 6,000 but less than 9,000 trees/ha.
  - 4 : More than 9,000 trees/ha.
- Dominant mangrove:
  - 1 : Buttonwood (Conocarpus erectus) most abundant
  - 2 : White mangrove (Laguncularia racemosa) most abundant
  - 3 : Black mangrove (Avicennia germinans) most abundant
  - 4 : Red mangrove (Rhizophora mangle) most abundant

8.2 (c) Statistical analyses

Multi-level categorical data such as these have unequal intervals, which can be problematic in statistical analyses (StatSoft 2002). The effect of this problem was tested by entering a set of corresponding binary variables, which were created by dummy-coding the scored variables, into the same cluster analysis described below. The result of Hierarchical Cluster Analysis using dummy-coded variables was the same as the result using multi-level categorical variables except for the group assignment of one pond, SIN, which had several unique characteristics. It was therefore concluded that the problem of unequal intervals did not bias the results of this classification analysis.

All 7 of the scored variables described above were known in 14 ponds, BAN, BEL, BLU, BON, FLA, GUA, HAN, JOS, LEE, LON, NOR, RUN, SAN and SIN, which were entered into a Hierarchical Cluster Analysis (SPSS 1999) to identify groups of similar ponds. SAL was not included because it lacked mangroves. Cluster analysis using the Squared Euclidian Distance method returned a range of solutions from 2 to 5 clusters. The best solution (see Table 8.1) was concluded to be one with the least number of clusters after which the addition of new clusters did not substantially change group associations.

Principal Components Analysis (PCA), using SPSS (1999) was performed to assess the importance of each variable in distinguishing between groups (see Section 8.2 (b)). The PCA was conducted using varimax rotation with Kaiser normalization (StatSoft 2002), extracting factors with eigenvalues greater than one. A scree plot was also used to evaluate the adequacy of the number of factors extracted. Bartlett's test of sphericity ($p = 0.000$), which assessed the degree of correlation between variables in the population correlation matrix, and the Kaiser-Meyer-Olkin test (0.76), which measured sampling adequacy (StatSoft 2002), indicated that factor analysis was appropriate for the matrix of 7 categorical variables.

Correlation coefficients were used to find redundant variables; one member of each pair having a correlation coefficient greater than 0.6 was removed from the classification model. The rotated component matrix produced by PCA was used as a guide to decide which of a pair of redundant variables was least useful in describing the variation between groups. Variables that loaded highly on one component and minimally on other components were considered to be most useful in discriminating between groups of ponds (see Section 8.2(b)).

Factor scores calculated by PCA for each pond were graphed using a scatter plot (see Figure 8.1), and the separation and clustering of ponds was compared with the results of hierarchical classification analysis. Points representing single ponds that fell well outside of all clusters were identified as outliers.

The final classification model (see Section 8.2 (c)) was based on the groupings predicted by the hierarchical cluster analysis using a minimum number of variables selected by their performance in the PCA.

8.3 Results and discussion

8.3 (a) Pond groupings

Ponds were classified using a set of 7 categorical variables selected from an initial set of 21 variables as described in Section 3.5 (a). These variables were: benthic producer (the most common type of benthic photosynthetic community, Figure 6.3), mangrove density (the number of mangrove trees per hectare, Appendix D), dominant mangrove species (Table 4.3), tidal influence/seawater inflow (which included tidally driven water level fluctuation as well as degree of sea connection, Table 4.1 and Table 4.3), sediment type, inundation period (Table 4.1), and salinity (Table 5.1). Table 8.1 shows the data set used in the classification analyses; it includes 14 ponds for which all 7 variables were known.

8.3 (a.*i*) Hierarchical Cluster Analysis

Hierarchical Cluster Analysis provided 4 alternative solutions ranging from 2 to 5 groups of ponds. The 2-cluster solution assigned HAN, LEE, NOR and SAN to one cluster (Group A, Table 8.1) and all other ponds to a second cluster. A 3-cluster solution split the latter group, with one cluster containing BLU, GUA, JOS, LON, RUN and SIN (Group B, Table 8.1) and another containing BAN, BEL, BON and FLA (Group C, Table 8.1). A 4-cluster solution reassigned LON to a new cluster, and a 5-cluster result reassigned SIN to a new cluster. The 3-cluster solution was accepted as the most representative because further divisions each reassigned only one pond.

Table 8.1 Pond groupings identified by Hierarchical Cluster Analysis. Variables and character scores are defined in Section 3.5 (b).

Group	Pond	Inund.	Tidal/ Sea-infl	Salin.	Sedi-ment	Prod-ucer	Mangr. density	Dom. mangr.
Group A	HAN	2	0	1	1	0	2	1
	LEE	2	0	1	1	0	2	1
	NOR	2	0	1	1	0	2	2
	SAN	2	0	1	1	0	2	1
Group B	BLU	3	1	2	2	1	4	3
	GUA	4	0	2	1	1	4	2
	JOS	3	0	1	1	1	4	3
	LON	3	2	2	1	2	3	3
	RUN	3	1	2	2	1	4	2
	SIN	4	1	1	3	0	4	4
Group C	BAN	4	0	3	3	3	2	1
	BEL	4	3	4	3	3	2	2
	BON	4	4	2	3	3	3	1
	FLA	4	4	3	4	3	3	3

The resulting pond groupings corresponded with Williams' 1998 classification of saline water bodies into permanent, intermittent and episodic water bodies, except that no episodic ponds occurred and that intermittent ponds were represented by 2 groups. Williams limited his classification to inland salt lakes, but these results show that his criteria may be applied to coastal ponds as well. His argument that only one type of saline water body should occur under particular climatic conditions, however, fails when coastal ponds are included because seawater inundation affects permanence. For this reason, permanence (inundation period) must be used in combination with other variables to distinguish among groups of salt ponds in the BVI.

8.3 (a.*ii*) Principal Components Analysis

Principal Components Analysis (PCA) extracted 2 components with Eigen values of 3.6 and 1.9. These components explained 78% of the total variance in the data set. Component scores assigned to each pond by PCA separated ponds into 3 groups (Figure 8.1) that corresponded with the groups identified by Hierarchical Cluster Analysis (Table 8.1). Groups A and B were separated by component 2, on which mangrove density and dominant mangrove loaded maximally in the rotated component matrix (Table 8.2). SIN appeared as an outlier to Group B. Group C was separated from groups A and B by component 1, upon which the variables inundation period, tidal influence/seawater inflow, salinity and sediment type loaded maximally.

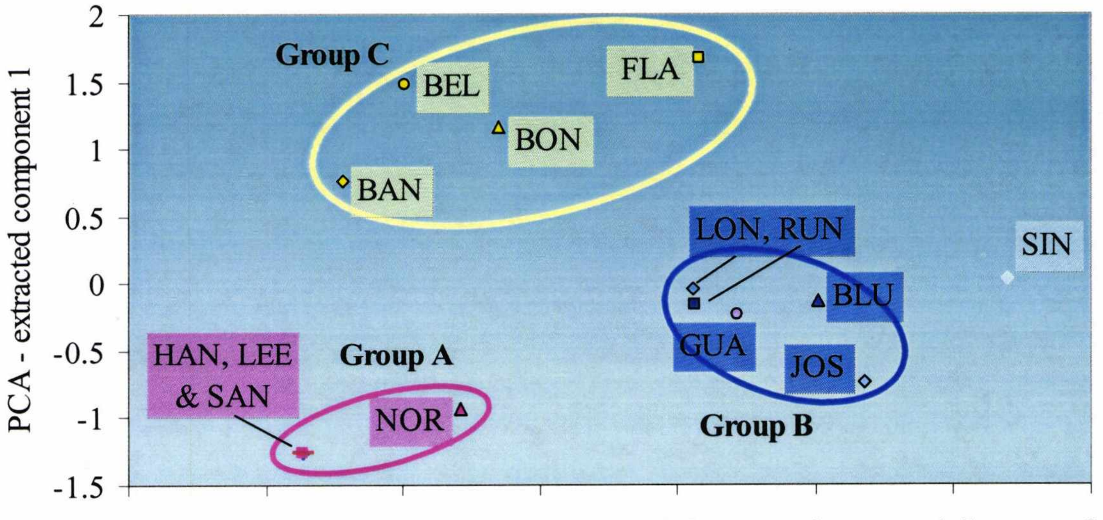


Figure 8.1 Grouping of ponds by PCA factor scores

8.3 (b) Performance of classification variables

PCA analysis was also used to evaluate the performance of the classification variables in grouping ponds.

Tidal influence/seawater inflow and sediment type performed better on component 1 than other variables, which also loaded on component 2 (Table 8.2). The importance of tidal influence/seawater inflow, as indicated by the PCA results, confirmed the value placed on this variable by Gunter (1967) and Por (1985). Sediments have not been used previously for classifying hypersaline water bodies but their importance to hypersaline communities has been demonstrated by Guerrero et al. (1994) and Waterman et al. (1999). Sediment type, despite performing well in the PCA, was somewhat redundant, being correlated with salinity (0.67), with inundation period (0.76) and with tidal influence/ seawater inflow (0.72, Table 8.3). It remains an important variable, however, because it is simpler to measure than tidal influence. In the absence of tidal data, sediment type should provide enough information to be used along with inundation period and dominant mangrove to classify new ponds.

Salinity did not perform well as it loaded on both component 1 and component 2, indicating that salinity was not as useful as other variables for separating groups of ponds. In addition, salinity had the undesirable property of being correlated with other variables. Salinity was correlated with inundation period (0.68), with tidal influence/seawater inflow (0.61) and with sediment type (0.67, Table 8.3).

Table 8.2 PCA rotated component matrix

	Loading on Component	
Variable	1	2
Inundation period	0.855	0.195
Tidal influence/seawater inflow	0.845	-7.04×10^{-2}
Salinity	0.842	-0.347
Sediment type	0.896	-8.31×10^{-3}
Benthic producer	0.785	0.124
Mangrove density	-3.87×10^{-2}	0.939
Dominant mangrove	5.75×10^{-2}	0.925

Table 8.3 Correlations between variables

	Inund.	Tidal inf.	Salinity	Sediment	Ben. prod.	Mang. den.
Tidal influence/ seawater inflow	0.57*					
Salinity	0.68*	0.61*				
Sediment type	0.76**	0.72**	0.67*			
Benthic producer	0.73**	0.74**	0.87**	0.70*		
Mangrove density	0.40*	0.06	-0.10	0.07	-0.05	
Dominant mangrove	0.34	0.20	0.01	0.22	-0.02	0.68*

* $= p < 0.05$
** $= p < 0.01$

Both mangrove density and dominant mangrove performed well in that their loadings were very high on component 2 and very low on component 1, but these variables were also correlated with one another (0.68). Dominant mangrove is likely to perform more consistently in assigning new ponds to groups because it is easier to measure and because it will vary less than mangrove density when different measurement techniques are used. The use of dominant mangrove as a classification variable is further supported by Lewis's (1990) observation that salt ponds in Puerto Rico and the U.S. Virgin islands may be distinguished as being dominated by black mangroves or by white mangrove and buttonwood, though mangrove forests around salt ponds are more variable than implied by Lewis (see Section 4.2 (d)).

Inundation period showed mediocre performance in the PCA, loading mostly on component 1 but also on component 2 (Table 8.2). However, this variable fits the pond groupings defined by cluster analysis. Group A ponds (Table 8.1) were all inundated for less than 6 months/year; Group B ponds, with the exception of SIN, were all inundated for more than 6 months but less than 12 months/year; and Group C ponds were all permanently inundated. Therefore, dominant mangrove, inundation period, sediment type and tidal influence/seawater inflow are concluded to be the most reliable of the classification variables used in this work.

8.3 (c) A practical guide to classification of salt ponds

Using Discriminant Function Analysis, it is possible to derive mathematical formulas into which character states can be entered in order to classify new ponds. However, a mathematical formula is not as practical and may not be as discriminating as a descriptive guide. The following guide to salt ponds is designed for practical field use and may be modified as new ponds are described. Ranges for classification parameters are based on the distributions observed in this study, but, where possible without sacrificing discrimination acuity, they have been expanded to accommodate greater variation likely to be found in new ponds. The classification nomenclature used is modelled after the hydrological categories of Williams (1998), but his "intermittent" water bodies, which dry seasonally, were split into "temporary ponds" and "annual ponds" and his "episodic" water bodies were not included. Using the following guide, predictions about hydrology, chemistry and biology can be made from patterns observed in comparable ponds. Such patterns are described for each group below.

8.3 (c.*i*) Temporary ponds

Examples: HAN, LEE, NOR and SAN

Temporary ponds (Group A, Table 8.1) are dry for more than 6 months/year and are inundated only after rainfall. Water is continuously present for less than 4 months at a time, and these ponds dry and fill repeatedly within single years. Water level does not respond to tidal changes in sea level, and sediments are composed of sandy mud. Mangrove forests around temporary ponds are normally dominated by buttonwood but in some cases white mangrove may prevail, and mangrove density between 1,000 and 6,000 trees/ha. is normal. Ruppia may occur at times when water is maintained for several months. Average salinities should be less than 60 ppt, but further sampling is needed to verify the average salinities of this group (see Section 3.5 (b)).

8.3 (c.*ii*) Annual ponds

Examples: BLU, JOS and RUN

Water in annual ponds (Group B, Table 8.1) is present for more than 6 months per year. Annual ponds have no permanent, direct connection with the sea. Some show tidally influenced changes in water level while others do not. Sediments are mostly sandy mud, but patches of organic mud may exist. GUA was an exception in this study because its water level was artificially maintained (see Section 4.2(a.i)). Either black mangrove or white mangrove dominates the mangrove forest around annual ponds, but all mangrove species may be present. Mangrove forests characteristically have tree densities greater than 8,000 trees/ha.

These ponds regularly develop meadows of Ruppia grass during periods of lower salinity. Average pond salinities are normally between 60 and 90 ppt, though some may have average salinities below 60 ppt (e.g. JOS).

8.3 (c.*iii*) Permanent ponds

Examples: BAN, BEL, BON and FLA

Permanent ponds (Group C, Table 8.1) never completely dry, though water level and pond size typically fluctuate. They may be directly connected with the sea (e.g. BON and FLA), completely isolated from the sea (e.g. BAN) or fed by a seawater seep (e.g. BEL). All permanent ponds except BAN were found in this study to exhibit tidal changes in water level. Sediments in permanent ponds are generally composed of loose organic mud, which may be covered by a hard gypsum crust as at FLA. Mangrove densities range between 1,000 and 8,000 trees/ha. and may be dominated by any species except red mangrove. Blue-black BMC and/or red floc occur as benthic producers in permanent ponds, and these microbial communities are unique to this group of ponds. Average salinities in permanent ponds are higher (>80 ppt) and often more variable (see Table 5.1) than in other groups.

8.3 (c.*iv*) Unclassified ponds and outliers

SIN was identified as an outlier in the PCA analysis (Section 8.2 (a.ii)). It was also readily separated from Group B ponds by Hierarchical Cluster Analysis in the 5-cluster solution (see Section 8.2 (a.i). SIN had a unique combination of characteristics, including permanence combined with low salinity (mean = 44 ± 8), organic mud sediments and, most particularly, a fringing forest dominated by red mangroves. These characteristics reflect its unique hydrology (see Section 5.2 (a.iii)). A pond on Great Thatch Island and a pond on the northern side of Necker Island, which were surveyed once each in 1998 and 1988, respectively, showed similarity to SIN in having fringing forests dominated by red mangrove, near seawater salinity, and organic mud sediments. Further sampling in such ponds is necessary to determine whether they represent a cohesive group.

LON also exhibited several characteristics that were unique among the annual ponds (Table 8.1). These included an intermittent sea connection, low tree density (6,500 trees/ha.) and a producer community dominated by green BMC. LON's association with annual ponds was weak, as indicated by its isolation in the 4-cluster solution of Hierarchical Cluster Analysis (see Section 8.2 (a.i).

WB, which was not included in the classification analysis due to a lack of mangrove density data, shared several unique characteristics with LON, including an intermittent sea connection and a producer community dominated by Green BMC. Together, LON and WB may represent a fourth (or fifth) group of ponds that are characterized by an intermittent sea connection and presence of Green BMCs. These ponds rarely support Ruppia and never form the vast Ruppia meadows that are typical in other annual ponds.

Several other ponds that were not included in the classification analysis can be evaluated using the guide presented. Despite a lack of mangrove data, RED can be grouped with permanent ponds because it never dried and because it supported red floc BMC. It also had high average salinity (160 ppt), and its water level fluctuated tidally. A hard gypsum crust, as in FLA, covered the sediments at RED. Manhead pond and PTP also showed affinities with permanent ponds, as they never dried, they did not support Ruppia meadows, and they were connected with the sea. However, sediments in these ponds were sandier than in other permanent ponds, and PTP did not support blue-black BMCs. Mangrove data were not collected at these ponds.

SAL shared with BEL the unique character of having a seep through which seawater entered. Salinities in these 2 ponds were very high (mean >150 ppt). SAL, however, neither developed a benthic producer community nor supported a fringing mangrove forest. No other salt pond was found lacking a fringing mangrove forest. As a result, SAL remains unique and cannot be assigned to any of the groups defined here.

The classification system presented here is unique among those for saline water bodies in the following ways:

1. This classification system incorporates several variables that are relatively simple to measure and remain consistent regardless of when they are measured (unless a pond has experienced physical changes between measurements, such as dredging, filling, or other processes that disrupt hydrology of mangrove forests).
2. Salinity is not considered an important distinguishing variable because of its high seasonal variability within ponds.

3. Characteristics of surrounding mangrove forests are considered to be important classification variables because groups of ponds differ in both tree density and species composition.

This chapter presented a statistical evaluation of the application of data presented in previous chapters to a scheme of ecosystem classification. It presents a unique classification system for salt ponds based on a reduced set of variables. The following chapter discusses the application of this study's results to wider scientific understanding of coastal hypersaline habitats and, in particular, to their management as ecosystems.

Chapter 9: Discussion

9.1 Geological formation of salt ponds

The hydrological variation observed among salt ponds (Chapter 4) reflects a trend from high connectivity with the sea to complete isolation from the sea. This trend is most clearly defined when the geomorphologies of bays and lagoons are considered. Completely open bays, or bights, lie at one extreme, but most bays are partially restricted by coral reefs that stretch across their entrances from one or both sides. Mangrove trees grow on the exposed tops of these coral reefs, particularly in areas sheltered from strong wave energy. Salt ponds appear to be only a small step in further isolation of a bay from the sea, as was noted by Lewis (1990).

The existing coastal morphologies, sediment characteristics, and vegetation types in wetlands of the BVI suggest a pattern of geologic evolution from shallow coastal marine waters to salt ponds and eventually to dry land. Such hydrological transformations are typical of estuarine and freshwater wetlands (Barbier *et al.* 1997), and mangrove ecosystems, in particular, are known to be dynamic ecosystems (Kathiresan & Bingham 2001).

The following sections describe a scenario for the geologic formation and eventual senescence of salt ponds on Caribbean islands. This is the first detailed description of salt pond formation in the Caribbean (Gene Shinn, pers. comm. 2001), and it is based on the patterns of hydrological variation in BVI salt ponds observed during this study. Future analyses of core sediment samples from multiple ponds will be required to confirm the patterns and processes proposed here.

9.1 (a) Reef crest formation

Many Caribbean reefs are actively prograding due to the rapid growth of *Acropora palmata* and *A. cervicornis*, which contribute to reef growth rates of up to 10 mm/yr (Lidz & Shinn 1991). This rate exceeds that of current sea level rise (2.3 ± 2.6 mm/yr) in the Caribbean (Ellison & Farnsworth 1996). Actively prograding reefs, which often form across the entrances to bays, may break the sea surface and form an exposed reef crest, as was observed over the course of 30 years in St. John, USVI (Cox *et al.* 2000). The presence of the reef crest creates a low-energy environment on the landward side, restricting sediment transport out of a bay (Hemminga *et al.* 1994). Waves breaking on the seaward side of the reef throw up coral rubble and sand in a process that forms a high berm by building up the original reef crest.

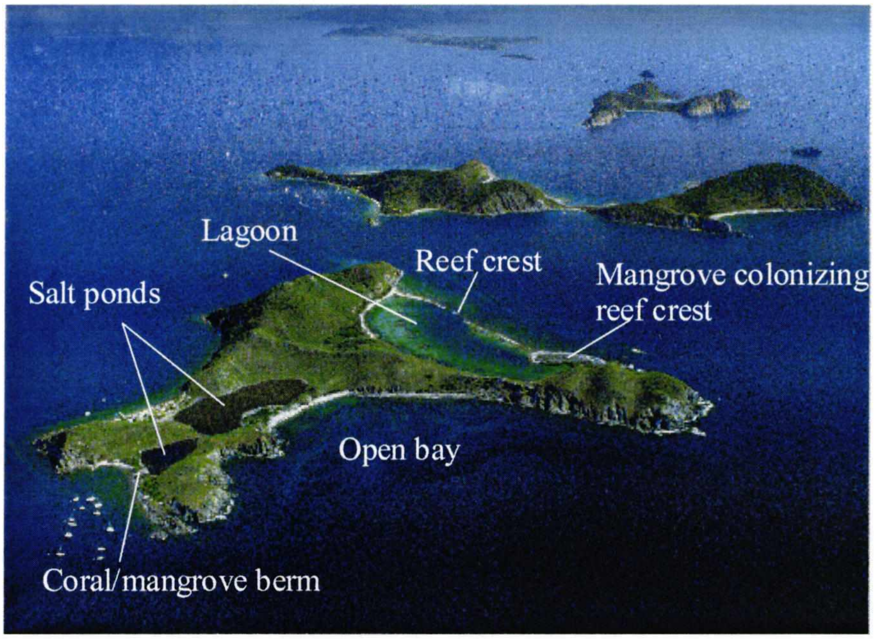
9.1 (b) Lagoon formation by mangrove growth and sediment accretion

Red mangroves colonise reef crests (Ellison 2000; Ellison & Farnsworth 1996), forming complex root networks that trap sediments and stabilize the berm (Ellison & Farnsworth 1996). Furukawa *et al.* (1997) showed that mangroves could trap 80% of the suspended sediments brought in from coastal waters on flood tides, and the ability of mangroves to build land by sediment accretion is well documented (Blasco *et al.* 1996; Kathiresan & Bingham 2001; Turner & Lewis 1997). Furthermore, McKee & Faulkner (2000) demonstrated that mangrove peat formation can drive vertical accretion that allows mangrove cays to keep pace with rising sea level.

As the processes of reef growth, mangrove colonization, sediment accretion and peat formation continue, the mangrove-vegetated berm expands across the bay entrance, restricting seawater flow into the bay and forming a lagoon. Restricted circulation encourages sedimentation within the lagoon by preventing the escape of sediments washed in from mountainous hillsides (Lugo & Snedaker 1974) and also by preventing the escape of sand washed into the lagoon by storm waves. Sedimentation leads to increasingly shallow water. Cox *et al.* (2000) reported a sedimentation rate of 3.6 cm/year in a back-reef lagoon in St. John (USVI), which at the end of their 30-year study (1998) was only 0.4 m deep.

9.1 (c) Lagoon closure

The volume of seawater flushing declines as sedimentation creates a progressively shallower lagoon. Eventually, sand deposits may block the entrance to a lagoon (Hodgkin & Hesp 1998). A blocked lagoon may periodically open when runoff waters blow out the accumulated sand deposits, as has been described at Great Salt Pond in Jamaica (Bacon & Alleng 1992) and at several lagoons in Vieques (Lewis 1988). Eventually mangroves grow across the lagoon entrance, cutting off direct water flow from the sea, and thus forming a pond. Lagoons in several stages of progression towards salt pond formation are shown in Figure 9.1.



Aerial photo by Jim Sheiner, 2001 (BVI Calendar)

Figure 9.1 Stages in the transformation of a bay to a salt pond illustrated on Salt Island, BVI

Sediments carried in runoff waters continue to settle throughout the pond phase. Benthic microbial mats (BMCs) can fix these sediments and decrease erodibility by secreting extracellular polymeric substances that bind clay and silt particles (Stal 1994; Wolanski 1995). *Ruppia* meadows can also accelerate sedimentation by trapping sediment particles in their root systems (Kantrud 1991). Sedimentation leads to gradual filling, which isolates the pond from through-ground seawater seepage and tidal influence. Water in the resulting shallow basin, which has been elevated by sedimentation, then evaporates to dryness during extended periods of dry weather.

9.1 (d) Evidence that ponds are former mangrove lagoons

This scenario of pond formation is supported by the results of a single sediment core taken from a salt pond in the U.S. Virgin Islands (IRF 1977). This core study showed that the most recently deposited layers were silt, washed by runoff water from the hillsides into the pond. Layers of organic muck were found between silt layers, and these were the remains of microbial mat growth within the pond. Occasional sand layers occurred among the layers of silt and organic muck, and these probably formed when large waves, from violent storms, threw sand over the berm and into the pond. The deepest and oldest layer was calcareous sand from the original bay bottom.

9.1 (e) Rate of salt pond formation and senescence

The geological processes necessary to create a salt pond (e.g. coral reef growth and sediment build-up by mangroves) are relatively rapid (Ellison & Farnsworth 1996; Lidz & Shinn 1991). Existing salt ponds, therefore, are not only geologically recent habitats but also temporary ones. The entire process of salt pond formation may require less than 6,000 years (Gene Shinn, pers. comm. 2001).

9.1 (f) Isolation from seawater causes hypersalinity

Prolonged closure of a lagoon leads to increasingly severe hydrological conditions (Hodgkin & Hesp 1998). Constant near-seawater salinity is characteristic of the lagoon phase because seawater flushing prevents the accumulation of salts. During the early pond phase, however, salts are often added by seawater input but are rarely flushed out, and accumulation of these salts leads to extreme hypersalinity. Ponds in later stages of this geological progression are completely isolated from seawater input, and salts that accumulated in earlier phases are gradually leached out by rainwater. Thus, late-phase ponds tend to have lower salinities than early-phase ponds. Both early- and late-phase ponds experience great salinity fluctuations in response to rainfall and evaporation (see Section 5.2 (a)).

9.1 (g) Mangrove distributions reflect hydrological transformations

Mangrove distributions and species composition respond to hydrological changes (Kathiresan & Bingham 2001). Red mangrove is predominant during the lagoon phase, but new edaphic gradients established in the pond phase favour the establishment of other mangrove species (McKee 1995). Lewis (1990) suggested that salt ponds that have long been isolated from tidal flow are dominated by white mangrove and buttonwood, and his observations are supported by the results of this study (see Section 4.2 (d)).

Mangrove distributions reflect hydrological differences among BVI salt ponds. Species composition of forests fringing the ponds, for example, was found to be a good indicator of the degree of sea connection in a pond (section 4.2 (*d.ii*)), and the dominant mangrove at each pond was an important variable in classifying ponds.

All permanent ponds and some annual ponds retained a small proportion of red mangroves in their fringing forests, while temporary ponds did not. These remaining red mangroves were sometimes clustered in small but dense patches, which were highly indicative of tidal influence within ponds (see Section 4.2 (d.*iv*)). The relationship found between the distribution of red mangroves and pond hydrologies indicates that mangroves will be useful in identifying hydrological variation at very fine geographic scales, as first suggested by Blasco *et al.* (1996).

9.1 (h) Pond classification system corresponds with hydrological transformations

The classification system presented in Chapter 8, which was based on variables ordered by increasing isolation from the sea, reflects the geological evolution of ponds proposed here. This classification system provides a framework that can be applied to the conservation and management of salt pond ecosystems in the BVI and other Caribbean islands.

Permanent ponds are early-phase ponds that are deeper and lower (bottoms below sea level) than other ponds, and for the most part, they receive regular seawater inputs. These ponds can be identified by the following characteristics: permanent inundation, organic sediments, benthic microbial communities, mixed mangrove forests, tidal influence (normally), and high but variable salinity.

Annual ponds are late-phase ponds that are not connected with the sea but may still receive occasional seawater inputs and are at or very near sea level (at the pond bottom). These ponds can be identified by the following characteristics: complete desiccation from one to 5 months during the dry season, no direct sea connection, sandier sediments and generally lower salinities than permanent ponds, and fringing forests dominated by white or black mangroves.

Temporary ponds are senescing late-phase ponds that have lost all connection with the sea and are above sea level. These ponds can be identified by the following characteristics: multiple desiccation and inundation events each year, with desiccated periods exceeding inundated periods, no sea connection or tidal influence, sandy sediments, and fringing forests dominated by buttonwood or white mangroves.

Rains remove salts from temporary ponds, allowing forest vegetation to colonize the pond edges. Encroachment of dry forest vegetation reduces the area of these ponds, which therefore tend to be small. As leaching proceeds, dry forest eventually consumes these ponds. Much of the flat agricultural land that occurs at the bottom of valleys of the BVI may have originally formed via the sedimentation of salt ponds.

9.2 Community interactions

Coastal hypersaline waters that were recently connected with the sea were once thought to contain only euryhaline marine organisms, in contrast with inland hypersaline waters that contained freshwater-derived species (Bayly 1972; Carpelan 1967; Por 1972). The biota found in BVI salt ponds, however, is similar to that found in other hypersaline systems, whether inland or coastal. With the exception of calanoid copepods, cladocerans, and amphipods, BVI salt ponds contain all of the major groups (anostracans, cyclopoid and harpacticoid copepods, ostracods, insects, rotifers and ciliates) that have invaded inland hypersaline waters (Bayly 1972; Hammer 1986; Hart *et al.* 1998; Simpson *et al.* 1998; Williams 1998). Crustaceans and insects dominate the aquatic communities of BVI salt ponds, and species representation is, not surprisingly, most similar to that described for Caribbean salterns (Kristensen & Husher-Emeis 1972). The list of species identified in this study (Table 6.1) is the most comprehensive yet reported for any Caribbean salt pond, and it is likely to represent Caribbean salt ponds in general. The species found are generally widely distributed (see Section 6.2 (a.*ii*)).

Overall, BVI salt ponds supported fewer aquatic animals than has been reported in hypersaline water bodies elsewhere. The absence of euryhaline species of calanoid copepods, cladocerans, and amphipods may result from the failure of these fresh-water derived taxa to disperse and colonize the small and distant BVI archipelago. BVI salt ponds, therefore, represent an exquisitely simplified aquatic food chain. In its simplicity, this aquatic system provides a model for understanding species interactions in hypersaline ecosystems.

9.2 (a) Grazers and detritivores

Most aquatic animals represented in BVI salt ponds are grazers or detritivores. *Cletocamptus* and other benthic harpacticoids graze diatoms and organic detritus attached to sediment particles (Des Marais 1995; Dexter 1995). *Trichocorixa* is a detritus feeder as well (Balling & Resh 1984; Hungerford 1948; Jang & Tullis 1980; Pennak 1978; Simpson *et al.* 1998). *Ephydra* is benthic and polyphagous, consuming cyanobacteria, algae, and detritus (Foote 1995; Larsen 1980). Fiddler crabs (*Uca burgersi*) feed on benthic algae and detritus from sediments both on the shores and within ponds.

Artemia is a planktonic filter feeder that captures particles (mostly algal & bacterial) from a few micrometers up to approximately 50 μm (Persoone & Sorgeloos 1980). Rotifers and ciliates in saline waters are also primary picoplankton grazers (Castenholz 1994). Rotifers filter algae less than 12 to 15 μm in size (Walker 1981). Kristensen & Hulsher-Emeis (1972) suggested that rotifers and *Artemia* in Caribbean salterns compete for food and that this competition can eliminate *Artemia* under some conditions. Rotifers were observed infrequently in BVI ponds and they never occurred simultaneously with *Artemia*. However a similar competitive argument may apply to the highly significant negative relationship found between ciliates and *Artemia* in BVI ponds (see Section 6.2 (g)).

Planktonic grazers can have a large impact on the suspended microbial portion of the food chain. Dense populations of *Artemia*, which can filter an estimated 99 ml/day per individual (Wurtsbaugh 1992), can reduce phytoplankton abundance by 90% (Hart *et al.* 1998). Efficient phytoplankton removal by planktonic grazers may enhance benthic production by eliminating water turbidity, which otherwise limits the development of BMCs and *Ruppia* meadows (Burke & Knott 1997; Kantrud 1991).

9.2 (b) Predatory interactions

Aquatic predators in BVI salt ponds are few, including only the abundant cyclopoid, *Apocyclops panamensis*, predatory beetles, which are uncommon, and fish, which are restricted in their distribution (see Section 6.2 (b.*i*)). *A. panamensis* appeared to be responsible for the rapid disappearance of *Artemia* populations at salinities below 80 ppt (see Section 6.2 (d.*ii* and g)). These cyclopoids may represent a terminal trophic level because they are too small (*ca.* 0.5 mm in length) to be captured by vertebrate predators, including filter-feeding flamingos, which do not capture particles smaller than approximately 1 mm (Jenkin 1957; Zweers *et al.* 1995). A lack of predators is also indicated by exponential growth, which *Apocyclops* exhibited in newly colonized ponds (see Section 6.2 (f)).

9.2 (c) Competitive interactions

Competitive interactions have been difficult to identify in hypersaline communities (Williams 1998), and they are generally thought to be rare due to the reduced number of species in these systems. Results presented in Section 6.2 (d.*ii* and g), however, suggest that both predation and competition limit the occurrence of high-salinity taxa when salinities drop below about 75 ppt. The negative relationship between the harpacticoids, *Cletocamptus deitersi* and *C. albuquerquensis*, in particular, appears to be one in which competitive dominance of *C. deitersi* limits *C. albuquerquensis* to salinities greater than 63 ppt, beyond the physiological tolerance of *C. deitersi*.

9.2 (d) Birds

Birds are major predators of invertebrates in hypersaline ecosystems (Bayly 1993; Hurlbert & Chang 1983; Kingsford & Porter 1994; Takekawa *et al.* 2001; Vareschi & Vareschi 1984), and they are abundant at BVI salt ponds (see Chapter 7). Most species recorded from BVI salt ponds are visual predators or shallow probers, and their effect on invertebrate communities is, therefore, restricted to shallow waters near pond edges (Hockey & Barnes 1997; Rehfisch 1994). Flamingos, in contrast, feed from the water column and benthos. A single flamingo can filter upwards of 20,000 litres of water per day (Bildstein *et al.* 1993). Flamingos are generalists and can subsist upon *Artemia, Ephydra*, molluscs, *Ruppia* seeds and even organic mud (Jenkin 1957; Rooth 1965; Zweers *et al.* 1995). *Dasyhelea* also appeared to be an important part of flamingo diets in BVI ponds. Flamingos can have a significant effect in decreasing the density of prey species (Glassom & Branch 1997), though they may be severely outcompeted when fish are present (Diamond 1987; Hurlbert *et al.* 1986). The population of flamingos was low (20 – 60 individuals) during this study, but their impact on the aquatic community structure of the Anegada ponds will become evident as their numbers increase.

Invertebrates in hypersaline water bodies represent an important food resource for resident and migratory birds worldwide (Kingsford & Porter 1994; Takekawa *et al.* 2001; Tanner *et al.* 1999; Warnock & Takekawa 1995; Williams *et al.* 1998). Invertebrates in BVI ponds, including benthic and planktonic insects, *Artemia*, and fiddler crabs, occupy a key trophic position in transforming these harsh hypersaline environments into important wildlife habitats.

9.3 Biotic responses to salinity fluctuations

Most taxa were distributed widely among ponds, and their distributions were primarily controlled by salinity fluctuations (see Section 6.2 (e.*ii*)). Factors that vary with salinity, such as dissolved oxygen and temperature, reached limiting levels for eukaryotic existence during periods of high salinity (see Sections 5.2 (b & d)). As evaporation intensified pond salinities, aquatic communities not only experience declining species diversity but they also experienced changes in species composition.

At any one time, a series of ponds displayed a range of salinities, and each contained a particular subset of species that corresponded with the pond's ambient salinity. *Artemia* and *Ephydra* formed a high-salinity faunal group, which was likely to be represented in ponds at 110 ppt or above. Ponds at salinities below 75 ppt contained a lower-salinity faunal group, including *Apocyclops,* Ciliophora and *Trichocorixa. Dasyhelea,* Ostracoda, Pisces and Rotifera were less consistent members of this lower-salinity faunal group. *Cletocamptus* was present in both high- and lower-salinity faunal groups. However, *C. deitersi* was likely to be associated with lower-salinity faunas and *C. albuquerquensis* with high-salinity faunas (see Section 6.2 (e.*iii*)). Faunal groups oscillated in response to changing salinities within ponds, and transitional faunas, including representatives of both high- and lower-salinity faunal groups, were present at salinities between 75 and 110 ppt.

The timing of faunal turnovers was linked to seasonal rainfall, but the characteristics of the turnovers differed among ponds. Some ponds became inhospitable to life during dry periods. Permanent ponds with especially high average salinities, BEL, RED and SAL, experienced extreme salinities combined with high temperatures and undetectable oxygen levels (see Sections 5.2 (b and d)) that eliminated all eukaryotic organisms. Temporary and annual ponds dried, leaving members of the lower-salinity faunal group with little habitat of appropriate salinity. During these times, small, shaded tidal pools within mangrove forests may serve as refuges for taxa that are intolerant of increasing salinities in permanent ponds. Such refuges may be especially important to aquatic insect populations (Williams 1985), which do not produce resistant cysts and must rely on dispersal for survival (Lahr *et al.* 1999).

When more benign conditions returned, aquatic fauna appeared quickly, but the composition of pond fauna after a large salinity change tended to differ from that before. Timms (1981), studying a series of Australian saline lakes of differing salinities, also observed seasonal changes in species composition. He found virtually no synchronization of these community changes among lakes, and he concluded that the factors causing changes in community structure operate independently among lakes, despite shared species and similar external factors. Aquatic communities in BVI salt ponds follow a similar asynchronous pattern. However, given the initial salinity and species composition of a pond, the response to a salinity change is predictable because the community will stabilize to represent a subset of taxa particular to the new ambient salinity within each pond.

Due to these oscillations in species composition, the number of planktonic taxa occurring in a pond over the long term was 2 to 4 times the number of taxa occurring at any one time (momentary species number). Green & Mengestou (1991) described similar differences between long term and momentary species number for rotifer populations in Ethiopian saline lakes.

9.4 Recommendations for salt pond conservation

9.4 (a) Habitat protection

Conservation of bird populations has long been a driving force in habitat conservation, especially in Europe and the United States. The Ramsar Convention, for example, was organised especially to protect waterfowl habitats (Davis 1994). Thus, the large number of migratory birds shown in this study to depend on salt ponds (Chapter 7) demands international interest in the implementation of effective salt pond conservation in the BVI and throughout the Caribbean islands where salt ponds are prevalent.

The particular importance of the Anegada Ramsar Site (and proposed national park) was illustrated by bird counts in which 40% of all the waterbirds counted (5,605) during this study were recorded from the Ramsar Site. Birds were especially abundant at FLA and PTP, which despite receiving only 17% of the total sampling effort, yielded 30% of the total number of birds counted.

Two other proposed national parks, BEL and WB, were exceptionally important to waterbirds. Twenty percent of all waterbirds were counted at BEL despite receiving only 11% of the total counting effort. Species richness (20) at WB was second only to JOS (21). It is recommended that the Anegada ponds, BEL, JOS and WB be given special protection as important waterfowl habitats.

The asynchronous oscillations in species composition observed within salt ponds during this study indicate that organisms inhabiting BVI salt ponds must depend on the existence of many ponds with varying hydrological characteristics. Bird populations, in particular, reflect this dependence on multiple ponds, as they tend to fly between ponds and may be following food resources that fluctuate within individual ponds. Necessity of dispersal and movement of both aquatic and terrestrial species between ponds indicates that BVI salt ponds exist as a network of habitats within a wider ecosystem rather than as a series of independent ecosystems.

This finding shows that the protection of individual ponds will be inadequate to conserve waterbird populations. Instead, a complex of ponds, throughout the BVI, is necessary to maintain the integrity of salt pond ecosystems. Priority should be given to annual and permanent ponds because they maintain aquatic communities for most of each year. Dependence of birds, and particularly of flamingos, on multiple ponds spread over enormous ecological neighbourhoods has also been shown for salt ponds elsewhere (Arengo & Baldassarre 1999; Britton *et al.* 1986; Jenkin 1957; Warnock & Takekawa 1995).

9.4 (b) Habitat rehabilitation

Ultimately, the combined impacts of marine pollution, sedimentation and the various consequences of global warming on near-shore coral reefs will prevent the formation of new lagoons and salt ponds. Langdon (2003), in reviewing the evidence for the effects of increasing concentrations of atmospheric carbon dioxide on coral reefs, concluded that a doubling or tripling of current atmospheric carbon dioxide concentrations in the next 50 to 100 years will result in a 25% decline in the calcification rate in reef building organisms. Under these conditions, it is unlikely that even the fastest growing coral reefs will continue to exceed sea level rise, a prerequisite to the formation of new salt ponds (see Section 9.1). Gardner *et al.* (2003) showed an 80% decline in live coral in the Caribbean over the past 3 decades. They cited a combination of causes, including disease, hurricane damage and reduced populations of algal grazers on reefs. The rate of coral decline in the Virgin Islands, however, is about half that in other Caribbean islands, and some corals, including *Acropora*, appear to be making a recovery (Gardner *et al.* 2003).

Meanwhile, accelerating development pressures claim more salt ponds each year. Loss of salt ponds, especially on Tortola, has already reduced the number of waterbirds in the BVI (Rowan Roy, pers. comm. 2002). There is, however, potential for rehabilitating wetlands that have been filled (Turner & Lewis 1997), and this has already been suggested for some Caribbean salt ponds (Lewis 1990). Where the original hydrological conditions of wetlands have been restored, recolonisation by plants and zooplankton may be rapid (Brockmeyer *et al.* 1997; Turner & Lewis 1997). Restoring the hydrological conditions of salt ponds in the BVI will require the removal of fill and solid wastes from ponds. Mangroves may need to be replanted, as they tend to be slow to recover in restored wetlands (Brockmeyer *et al.* 1997). Areas where such restoration may still be possible because no physical structures exist atop the fill include Brandywine Bay Pond (Tortola), Great Harbour Pond (Jost Van Dyke), Flamingo Pond at Coxheath (Tortola), Ross Pond (Cane Garden Bay), SIN and WB.

Local conservationists (e.g. Bert Lettsome, pers. comm. 2000) have suggested removing erosional sediments that have accumulated in existing ponds. This practise would effectively reverse the natural process of pond senescence (Section 9.1 (c)), but it may be necessary in light of accelerated sedimentation rates (Section 2.2 (a.*ii*)) and reduced potential for the formation of new ponds. Removal of erosional sediments should be used only as a very last resort in habitat management, and it is ill advised in ponds that contain benthic microbial communities. Disturbance of these BMCs will disrupt the microenvironmental gradients and nutrient transformations in the microbial consortia that sustain the benthic communities in some ponds (Paerl & Pinckney 1996). Opening ponds to the sea is also problematic because this practise allows the entrance of fish, which reduce zooplankton abundances and compete with waterbirds (see Section 9.2 (a.*iv*))

9.5 Summary and conclusion

This study has shown that salt ponds of the BVI are unique and highly variable ecosystems on which many species depend. This dependence ultimately includes human populations that require clean coastal waters and healthy marine ecosystems, which salt ponds help to maintain. The information presented fills a major gap in existing knowledge of Caribbean wetlands, and it will promote a better local and regional understanding of the value of salt ponds. Immediate and wholesale protection of salt ponds and all species of mangroves is necessary to ensure the survival of these ecosystems. The BVI must take immediate steps towards managing salt ponds to preserve the ecosystem services they provide. These steps should include drafting legislation that protects all wetlands, including those that are privately owned, and rehabilitating filled ponds.

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Appendix A
Sampling Dates and Times

1995							
BAN		**BEL**		**BON**		**FLA**	
31-Jan	04:30	28-Jan	14:45	19-Jan	16:20	19-Jan	12:30
27-Feb[f]	14:00	22-Feb	14:45	26-Feb	12:00	26-Feb	13:30
26-Mar	15:30	19-Mar	12:40	26-Mar	\	26-Mar[e]	10:30
26-Apr	17:20	26-Apr	15:00	30-Apr	10:40	29-Apr	14:50
13-May	17:30	13-May	11:00	30-May[f]	08:45	30-May	10:00
30-Jun	17:10	28-Jun	17:00	30-Jul	17:00	31-Jul	17:30
26-Jul	12:00	25-Jul[a]	10:00	27-Aug[f]	13:30	27-Aug	15:30
15-Aug	09:30	14-Aug[a]	10:30	24-Sep[k]	13:40	24-Sep[k]	11:30
04-Sep	15:30	17-Sep[f,k]	17:30	28-Oct	15:15	28-Oct	13:50
15-Oct	08:30	07-Oct	08:30	26-Nov	12:00	26-Nov	13:00
05-Nov	09:30	4-Nov[f]	14:45				
16-Dec	09:30	21-Dec	17:10				
GUA		**JOS**		**PTP**		**RED**	
13-Jan	\	29-Jan	10:00	20-Jan	09:00	20-Jan	13:00
04-Feb	09:45	20-Feb[c]	09:00	26-Feb	15:00	26-Feb	10:30
18-Mar	15:15	25-Mar[a]	13:45	26-Mar[c,e]	15:15	26-Mar	13:30
14-Apr	\	14-Apr[b,g]	\	29-Apr[a]	16:30	30-Apr	09:45
14-May	18:00	13-May[c]	13:45	30-May[a]	11:30	30-May	07:30
10-Jul[h]	18:30	7-Jul[b,i]	10:00	31-Jul	18:15	30-Jul	15:30
23-Jul	16:30	25-Jul[b]	12:00	27-Aug[a]	16:15	27-Aug	11:30
11-Aug	11:30	14-Aug[b,g]	15:30	24-Sep[k]	10:00	24-Sep[k]	15:00
23-Sep[k]	15:00	23-Sep[j,k]	12:30	28-Oct	17:00	28-Oct	16:00
14-Oct	14:00	7-Oct[j]	11:00	26-Nov	15:00	26-Nov	10:45
19-Nov	11:30	5-Nov[j]	07:00				
		16-Dec	12:00				

a water at sampling site was too low for plankton tow
b pond was completely dry
c plankton net was only half submerged because pond was shallow
d Length of plankton tow was 8 m instead of the normal 20 m
e Sample spilled; enough was retained to record p/a, but not included in density analysis
f No count of Uca burrows
g No bird count
h Bird count only
i Used as June sample
j Not included in logistic regressions due to salinity lower than 35 ppt
k Not included in logistic regressions because > 5 cm of rain fell over the previous 14 days
l Not included in logistic regressions due to salinity greater than 350 ppt
\ Time not recorded

1995 continued			
SAL		**WB**	
24-Jan	11:00	29-Jan	17:00
05-Feb	15:10	23-Feb	16:00
05-Mar	\	19-Mar[b]	16:45
8-Apr[l]	\	14-Apr[b,g]	\
14-May[l]	12:00	28-May[d]	18:00
8-Jun[l]	14:00	7-Jul[i]	10:40
28-Jul	16:00	26-Jul	13:30
16-Aug	11:00	15-Aug	14:00
30-Sep	15:45	9-Sep[j,k]	14:00
27-Oct	14:30	7-Oct[j]	12:30
30-Nov	15:00	05-Nov	11:00
		16-Dec	14:15

a water at sampling site was too low for plankton tow
b pond was completely dry
c plankton net was only half submerged because pond was shallow
d Length of plankton tow was 8 m instead of the normal 20 m
e Sample spilled; enough was retained to record p/a, but not included in density analysis
f No count of Uca burrows
g No bird count
h Bird count only
i Used as June sample
j Not included in logistic regressions due to salinity lower than 35 ppt
k Not included in logistic regressions because > 5 cm of rain fell over the previous 14 days
l Not included in logistic regressions due to salinity greater than 350 ppt
\ Time not recorded

Samples from 1991 - 2000, excluding 1995

BAN		Beef Is. Salt Flats		BEL		BLU	
12-May-91	\	08-Jul-93	\	20-Mar-91	\	19-Feb-99	09:45
29-Jul-92	\			29-Jul-92	\	24-Feb-99	22:00
08-Jul-93	\			14-Jul-93	\		
24-Jul-94	\			24-Jul-94	\		
20-Sep-98[h]	17:30			27-Feb-99	\		
14-Oct-98	06:00			02-Mar-99	18:00		
29-Oct-98[h]	06:15			07-Apr-99	\		
28-Jan-00	15:30			27-May-99	\		
20-Apr-00	09:30			20-Feb-00	13:00		
01-Jul-00	15:00			28-Apr-00	10:15		
11-Jul-00	13:00			10-Jul-00	12:10		
13-Aug-00	16:30			01-Sep-00	08:40		
BON		**FLA**		**Great Thatch Pond**		**GUA**	
13-Mar-91	\	13-Mar-91	\	18-Oct-98	14:30	10-Mar-91	\
26-Jul-92	\	09-Aug-98	07:00			16-Apr-91	\
02-May-99	\	02-May-99	16:30			15-May-91	\
16-Feb-00	15:30	16-Feb-00	\			18-Jun-91	\
22-Apr-00	11:00	21-Apr-00	16:30			18-Aug-91	\
21-Jul-00	16:00	20-Jul-00	17:00			30-Jun-92	\
03-Sep-00	20:30	04-Sep-00	10:30			03-Aug-92	\
						3-Jul-93[h]	\
						23-Aug-93	\
						16-Jul-94	\
						03-Aug-94	\
						20-Sep-98[h]	\
						18-Oct-98	06:00
						29-Oct-98[h]	\
						01-Jul-00	11:30
						14-Jul-00	07:15
						29-Jul-00	16:30
						19-Aug-00	06:40

g Not included in logistic regressions due to salinity lower than 35ppt

h Not included in logistic regressions because more than 5cm of rain fell over the previous 14 days

\ Time not recorded

(Table continued on following page)

Samples from 1991 - 2000, excluding 1995 (continued)

JOS		**LON**		**Manhead Pond**		**PTP**	
25-Jul-92	\	19-Sep-98[h]	15:20	02-May-99	\	02-May-99	\
14-Jul-93[g]	\	13-Oct-98	06:00	16-Feb-00	\	16-Feb-00	13:30
20-Sep-98[h]	18:20	29-Oct-98[h]	17:45			21-Apr-00	15:00
16-Oct-98	06:30	19-Feb-99	10:20				
29-Oct-98[h]	07:30						
19-Apr-00[g]	09:00						
26-Jul-00	08:45						

RED		**RUN**		**SIN**		**WB**	
02-May-99	\	10-Apr-99	\	28-Apr-00	08:30	12-Aug-94	\
22-Apr-00	10:30	19-May-00	\	31-Aug-00	10:30		
21-Jul-00	14:30						
04-Sep-00	21:45						

g Not included in logistic regressions due to salinity lower than 35ppt

h Not included in logistic regressions because more than 5cm of rain fell over the previous 14 days

\ Time not recorded

Hurricane data matrix

BAN (1995)		**BAN (1998)**		**LON (1998)**		**JOS (1998)**	
04-Sep	15:30	20-Sep	17:30	19-Sep	16:30	20-Sep	18:20
Hurricane Luis		*Hurricane Georges* -					
09-Sep	15:30	23-Sep	10:20	23-Sep	15:50	24-Sep	07:00
13-Sep	14:30	01-Oct	07:45	29-Sep	06:15	30-Sep	06:30
Hurricane Marilyn		08-Oct	07:45	07-Oct	06:15	08-Oct	10:40
17-Sep	13:00	14-Oct	06:00	13-Oct	06:00	16-Oct	06:30
23-Sep	09:45	23-Oct	16:45	23-Oct	17:20	23-Oct	17:45
27-Sep	17:30	29-Oct	06:15	29-Oct	05:45	29-Oct	\
01-Oct	08:30	07-Nov	08:00			08-Nov	\
05-Oct	16:30						
15-Oct	08:30						
25-Oct	14:30						
05-Nov	09:30						

GUA (1998)		
20-Sep	------------	*Hurricane Georges*
03-Oct	17:00	
12-Oct	06:45	
18-Oct	18:05	
25-Oct	17:45	
29-Oct	\	

1995: 5 September, 1995: Hurricane Luis
15 September, 1995: Hurricane Marilyn
1998: 21 September, 1998: Hurricane Georges

Appendix B
Water Chemistry Data:
Salinity, temperature, pH and dissolved oxygen

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
BAN								
21-May-91			128					
29-Jul-92			146					
08-Jul-93			110					
24-Jul-94			144					
31-Jan-95	16:30	clear	110	35		4		
27-Feb-95	14:00	overcast	100	27			3.8	90%
26-Mar-95	15:30	clear	160	36			4.8	
26-Apr-95	17:20	clear	200	34			0.8	36%
13-May-95	17:30	clear	220	37			0.6	
30-Jun-95	17:10	clear	190	39				
26-Jul-95	12:00	clear	170	33			1.2	43%
15-Aug-95	09:30	clear	160	34			1.6	53%
04-Sep-95	15:30	clear	120	39			1.2	
09-Sep-95	15:30	clear	76	35			3.5	73%
13-Sep-95	14:30	clear	78	35			2.6	57%
17-Sep-95	13:00	overcast	60	30			3.5	65%
20-Sep-95	18:00	clear	63	32			4	77%
23-Sep-95	09:45	overcast	65	30			3	57%
27-Sep-95	17:30	overcast	70	32			3.4	68%
01-Oct-95	08:30	part. cloudy	69	29				
05-Oct-95	16:30	clear	72	34				
15-Oct-95	08:30	clear	77	30			3.2	65%
25-Oct-95	14:30	part. cloudy	75	35				
05-Nov-95	09:30	clear	81	28				
16-Dec-95	09:30	overcast	87	26			3	61%
20-Sep-98	17:30		83	35		19		
23-Sep-98	10:20		64		8.0	33	5.7	
01-Oct-98	07:45		64		8.5	28	5.9	
08-Oct-98	07:45		68	19	8.5	41	4.7	76%
14-Oct-98	06:00		71	17	8.5	42	2.9	46%
23-Oct-98	16:45		60	20	8.5	32	5.9	92%
29-Oct-98	06:15		60	16	8.5	23	4.6	67%

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
BAN (continued)								
07-Nov-98	08:00		37	29	8.5	16	5.2	83%
10-Nov-98			57					
04-Jan-00	12:45	overcast		30			9	
28-Jan-00	11:15	clear	46	28			6	98%
28-Jan-00	15:30	part. cloudy	46	33		28	6	110%
20-Apr-00	09:30		82	27				
01-Jul-00	15:15	clear	89	33	8.4	52	5.9	130%
11-Jul-00	13:00	clear	92	33			5.9	130%
11-Jul-00	15:00	clear	93	34		59	6.1	140%
11-Jul-00	18:00	part. cloudy	90	32			5.8	130%
11-Jul-00	21:15	night	91	28	8.2		3.5	74%
12-Jul-00	07:00	clear	92	26	8.2	57	2.1	44%
12-Jul-00	09:00	clear	92	28			3.6	77%
13-Aug-00	16:30	clear	80	33	8.8	45	6.6	140%
13-Aug-00	20:45	night	80	31			5.6	120%
14-Aug-00	07:00	clear	79	26			2.6	50%
14-Aug-00	12:00	clear	80	31			5.5	120%
08-Sep-00	16:15	clear	77	37	8.6	59	7.8	
BEL								
21-Mar-91			120					
29-Jul-92			192					
14-Jul-93			216					
24-Jul-94			305					
28-Jan-95	14:45	clear	130	32		20		
22-Feb-95	14:45	clear	170	35			1	37%
19-Mar-95			160					
26-Apr-95	12:40	clear	350	33			0	
13-May-95	11:00	clear	130	38			1.4	
28-Jun-95	17:00	clear	310	41			0	
25-Jul-95	10:00	part. cloudy	310	37			0	
14-Aug-95	10:30	clear	100	39				
17-Sep-95	17:30	overcast	75	29			3	59%
07-Oct-95	08:30	clear	76	29			4	80%

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
BEL (continued)								
04-Nov-95	15:45	clear	83	33			7	150%
12-Dec-95	17:10	clear	86	30			6	130%
27-Feb-99			67					
02-Mar-99	18:00		70					
07-Apr-99			100				4	
27-May-99			160					
20-Feb-00	13:00	part. cloudy	65	29			4	74%
20-Feb-00	16:00	part. cloudy	65	30			5.6	110%
28-Apr-00	10:30		160	30			0.3	10%
10-Jul-00	12:15	clear	300	39			0	
10-Jul-00	15:00	clear	300	39			0	
10-Jul-00	18:00	clear	300	36	6.8	47	0	
23-Aug-00	18:30	part. cloudy	170	32	7.5	52	2	71%
01-Sep-00	08:40	clear	220	30	7.6	21	0.1	5%
BLU								
23-Jan-99	15:00		41					
18-Feb-99	07:30		71					
19-Feb-99	09:45		70					
21-Feb-99	12:00		79					
24-Feb-99	22:00		85					
02-Mar-99	13:30		105	nearly dry				
BON								
13-Mar-91			91					
26-Jul-92			87					
19-Jan-95	16:20	clear	75	33				
26-Feb-95	12:00	part. cloudy	90	30			4	87%
26-Mar-95		clear	110	31			3.4	85%
30-Apr-95	10:40	clear	120	32			3.4	89%
30-May-95	08:45	clear	120	29			3.2	82%
30-Jul-95	17:00	part. cloudy	88	35			4	91%
27-Aug-95	13:30	clear	110	34				
24-Sep-95	13:40	overcast	60	33			4	77%
28-Oct-95	15:15	clear	68	35			7	140%
26-Nov-95	12:00	part. cloudy	87	29			6	130%

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
BON (continued)								
02-May-99			72					
16-Feb-00	15:30	clear	65	31		51		
21-Apr-00	18:00		85					
22-Apr-00	11:00		78	29			4.5	90%
22-Apr-00	16:15		80					
21-Jul-00	16:00	clear	83		8.3	22	5.3	
21-Jul-00	22:15	night	84				4.7	
22-Jul-00	06:45	clear	82		8.2	20	3.3	
22-Jul-00	13:00	clear	84				4.8	
03-Sep-00	20:30	night	57	30			6.1	110%
05-Sep-00	07:15	clear	59	28			3.5	63%
05-Sep-00	09:20	clear	59	29	8.3	16	3.9	70%
05-Sep-00	15:30	overcast	59	33			6.2	120%
Budrock Pond, Anegada								
30-May-95	16:00	clear	290	36			0	
FLA								
13-Mar-91			98					
19-Jan-95	12:30	clear	79	32				
26-Feb-95	13:30	part. cloudy	92	30			4	89%
26-Mar-95	10:30	clear	120	30			4	110%
29-Apr-95	14:50	clear	160	36			3.6	
30-May-95	10:00	clear	140	31			2	59%
31-Jul-95	17:00	clear	110	34			2.8	72%
27-Aug-95	15:30	clear	120	33			1.2	32%
24-Sep-95	11:30	overcast	65	31			4	77%
28-Oct-95	13:50	clear	66	34			8	160%
26-Nov-95	13:00	clear	81	31			6	130%
08-Aug-98	12:30		89	32				
02-May-99			89					
16-Feb-00	16:30		77	29		76		
21-Apr-00	16:30	clear	130	35			5	150%
22-Apr-00	16:30		130					
20-Jul-00	17:00	clear	130	32	7.9	22	3.5	97%
20-Jul-00	21:00	night	120				3.5	

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
FLA (continued)								
21-Jul-00	05:45	clear	110		7.9	17	1.7	
21-Jul-00	10:30	clear	110				3.7	
04-Sep-00	10:30	clear	70	31			4.6	90%
04-Sep-00	15:00	clear	70	36	8.3	36	6.3	
29-Jul-00	16:30	overcast	72	28			6.7	130%
30-Jul-00	07:00	part. cloudy	59	25			3.4	57%
30-Jul-00	12:00	part. cloudy	60	30			5.1	94%
30-Jul-00	20:00	night	62	29			6.4	120%
31-Jul-00	06:50	clear	61	26	8	22	4.6	79%
01-Aug-00	11:35		57					
19-Aug-00	06:40	part. cloudy	73	26			1.8	33%
19-Aug-00	12:15	clear	70	34			8.7	180%
19-Aug-00	18:30	part. cloudy	72	35			8.2	170%
19-Aug-00	21:15	night	72	32			4.6	94%
20-Aug-00	15:40	clear	71	38			9.9	
Great Harbour Pond, Jost Van Dyke								
18-Oct-98			34		8	98		
Great Thatch Pond								
18-Oct-00			43		8.5	40		
GUA								
10-Mar-91			46					
19-Apr-91			72					
15-May-91			96					
18-Jun-91			95					
18-Aug-91			85					
15-Jul-92			49					
03-Aug-92			57					
03-Jul-93			58					
23-Aug-93			85					
16-Jul-94			100					
03-Aug-94			100					
13-Jan-95		clear	74	28		5		

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T ºC	pH	Turbidity (FAU)	[O_2] (mg/L)	[O_2] % Sat.
GUA (continued)								
04-Feb-95	09:45	overcast	80	27		10		
18-Mar-95	15:15	clear	79	31			10	210%
14-Apr-95		clear	140	36			6	
14-May-95	18:00	clear	92	38			6	
23-Jul-95	16:30	clear	120	36			5	
11-Aug-95	11:30	clear	100	35			5	130%
23-Sep-95	15:00	overcast	43	33			9	160%
14-Oct-95	14:00	clear	47	35			8	150%
19-Nov-95	11:30	clear	43	29			8	130%
02-May-98			78					
20-Sep-98			83	36		74	11	
03-Oct-98	17:00		61			16	11	
12-Oct-98	06:45		57	18	8.5	33	2.3	34%
18-Oct-98	06:00		62	22		42		
25-Oct-98	17:45		41	23	8.5	32	8.6	130%
29-Oct-98			40	23	8.5	43	10	150%
10-Nov-98	07:00	clear	28	29	8.5	20	5.9	89%
01-Jul-00	11:30		84	32	8.4	84	7.5	160%
09-Jul-00	17:00	clear	91	29				
14-Jul-00	07:15	clear	83	27	8.2	110	1.3	26%
14-Jul-00	09:50	part. cloudy	86	30			5.9	130%
14-Jul-00	12:00	part. cloudy	83	35			7.2	160%
14-Jul-00	15:30	clear	83	37	8.2	100	9.3	
14-Jul-00	18:00	clear	85	35			7.7	180%
15-Jul-00	11:15	part. cloudy	86	31			6.4	140%
15-Jul-00	16:50	clear	88	35			7.9	180%
15-Jul-00	21:00	night	88	30			4.4	96%
16-Jul-00	05:40	clear	88	26			0.9	18%
29-Jul-00	16:30	overcast	72	28			6.7	130%
30-Jul-00	07:00	part. cloudy	59	25			3.4	57%
30-Jul-00	12:00	part. cloudy	60	30			5.1	94%
30-Jul-00	20:00	night	62	29			6.4	120%
31-Jul-00	06:50	clear	61	26	8	22	4.6	79%
01-Aug-00	11:35		57					

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T ºC	pH	Turbidity (FAU)	[O$_2$] (mg/L)	[O$_2$] % Sat.
GUA (continued)								
19-Aug-00	06:40	part. cloudy	73	26			1.8	33%
19-Aug-00	12:15	clear	70	34			8.7	180%
19-Aug-00	18:30	part. cloudy	72	35			8.2	170%
19-Aug-00	21:15	night	72	32			4.6	94%
20-Aug-00	15:40	clear	71	38			9.9	
JOS								
25-Jul-92			60					
14-Jul-93			32					
29-Jan-95	10:00	clear	53	31		38		
20-Feb-95	09:00	clear	86	27			6	120%
25-Mar-95	13:45	clear	110	41				
13-May-95	13:45	clear	38	38			12	
25-Jul-95	12:00	clear	78	38				
23-Sep-95	12:30	overcast	24	31			12	190%
07-Oct-95	11:00	overcast	27	30			11	170%
05-Nov-95	07:00	part. cloudy	28	27				
16-Dec-95	12:00	clear	35	28			18	280%
06-May-98			65					
20-Sep-98	18:20		72	32		9		
24-Sep-98	07:00		25		8.5	32	5.4	
30-Sep-98	06:30		31		8.5	27	3.7	
08-Oct-98	10:40		38		9.0	7	6.9	
16-Oct-98	06:30		45	16	9.0	36	0.7	9%
23-Oct-98	17:45		12	18	6.5	25	8.7	98%
29-Oct-98	07:30		9	16	9	33	12.3	130%
08-Nov-98			12	31	8.5	36	8.7	130%
19-Apr-00	09:00	clear	25					
26-Jul-00	08:45	part. cloudy	120				3	
26-Jul-00	13:30	part. cloudy	120	38			8	
26-Jul-00	17:45	part. cloudy	130	32	8.8	230	4.2	120%
26-Jul-00	21:45	night	120				0.5	
27-Jul-00	07:00	clear	130	25			0.5	13%
24-Aug-00	11:00	partly cloudy	33	33				
24-Aug-00	16:00	partly cloudy	33	33	8.2	130	7.2	120%

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
JOS (continued)								
24-Aug-00	20:20	night	32	29			3.6	56%
25-Aug-00	07:00	clear	32	26			1.1	16%
18-Dec-00	16:50	clear	88					
LEE								
02-May-99			66					
LON								
19-Sep-98			130			20		
23-Sep-98	15:50		43		9	8	11	
29-Sep-98	06:15		48		9.0	17	4.75	
07-Oct-98	06:15		60	17	9.0	5	2.7	40%
13-Oct-98	06:00		63	17	9.0	9	3.2	48%
23-Oct-98	17:45		50	19	9.0	12	7.35	110%
29-Oct-98	17:45		40	17	8.5	6	3.1	40%
08-Nov-98			40	31	8.5	15	8.2	140%
19-Feb-99	10:20		84					
10-Apr-99			45		8.0			
31-Jan-01	15:35		56					
NOR								
30-Jul-00			9					
Manhead Pond, Anegada								
21-Apr-00	17:45		72					
22-Apr-00	11:15		70					
22-Apr-00	16:15		75					
21-Jul-00	16:45		85					
PTP								
20-Jan-95	09:00	clear	75	29		7		
26-Feb-95	15:00	part. cloudy	85	30			3.4	72%
26-Mar-95	15:15	clear	67	34				
29-Apr-95	16:30	clear	140	35				
30-May-95	11:30	part. cloudy	140	34				
31-Jul-95	18:15	clear	110	33			3.2	80%

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
PTP (continued)								
27-Aug-95	16:15	clear	120	32				
24-Sep-95	10:00	clear	65	30			4	75%
28-Oct-95	17:00	clear	46	32			7	120%
26-Nov-95	15:00		86	34				
02-May-99			70					
16-Feb-00	13:30	clear	48	29		12		
21-Apr-00	15:00		80	36				
RED								
20-Jan-95	13:00	clear	140	35		2		
26-Feb-95	10:30	part. cloudy	210	30			0.4	18%
26-Mar-95	13:30	clear	260	39			0	
30-Apr-95	09:45	clear	260	34			0.2	13%
30-May-95	07:30	clear	270	29			0.4	
30-Jul-95	15:20	overcast	180	35			1.2	48%
27-Aug-95	11:30	part. cloudy	220	34			0.6	30%
20-Sep-95	15:00	overcast	72	32			4.5	92%
28-Oct-95	16:00	clear	95	37			6	
26-Nov-95	10:45	overcast	130	29			5	140%
02-May-99			130					
16-Feb-00	15:00		97	32		290		
21-Apr-00	18:15		130					
22-Apr-00	10:30	part. cloudy	130	31			1.6	46%
22-Apr-00	16:15		140					
21-Jul-00	14:30	clear	160			27	2	
04-Sep-00	21:45	night	66	29	8.6		5.4	100%
05-Sep-00	07:00	clear	68	27			3.5	65%
05-Sep-00	09:30	clear	68	30			5.2	100%
05-Sep-00	15:40	overcast	68	33			7	140%
RUN								
10-Apr-99			45					
19-Apr-00	09:30		110	nearly dry				
01-Jul-00								
18-Dec-00	17:15		88					
31-Jan-01	15:25	clear	96					

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Date	Time	Weather	Salinity (ppt)	Water T °C	pH	Turbidity (FAU)	$[O_2]$ (mg/L)	$[O_2]$ % Sat.
SAL								
24-Jan-95	11:00	clear	300	33		0	0	
05-Feb-95	15:15		340	36			0	
05-Mar-95		clear	270	36			1	
08-Apr-95		clear	400	45				
14-May-95	12:00	clear	500	41			0	
08-Jun-95	14:00	clear	400	42			0	
28-Jul-95	16:00	clear	340	43			0	
16-Aug-95	11:00	part. cloudy	300	39			0	
30-Sep-95	15:45	clear	180	36				
27-Oct-95	14:30	clear	220	37			1.2	
30-Nov-95	15:00	clear	250	36				
08-Jul-00	12:00	clear	360	36	7.1	13	0	
SIN								
28-Apr-00	08:30	clear	51	28	8.0	34		
31-Aug-00	10:30	clear	46	34	7.8	30	5.2	95%
03-Feb-01			35					
WB								
12-Aug-94			47	37		2	1.7	
29-Jan-95	17:00	clear	38	33		6		
23-Feb-95	16:00	clear	42	35			10.6	190%
19-Mar-95	16:45	clear	65	33				
28-May-95	18:00	clear	85	34			8	180%
07-Jul-95	10:40	clear	67	34			4	80%
26-Jul-95	13:30	clear	62	35			5	100%
15-Aug-95	14:00	clear	60	35			5	510%
09-Sep-95	14:00	clear	32	36			8	
07-Oct-95	12:30	overcast	27	35			10	170%
05-Nov-95	11:00	part. cloudy	40	32				
16-Dec-95	14:00	overcast	53	28			16	280%
20-Apr-00	10:30		77					

data in shaded cells were excluded from calculations of means (see Section 3.3 (h))
blank cells represent cases in which a parameter was not measured

Appendix C

Nutrient Data:

Nitrates, nitrites, ammonia and phosphates

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (µg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
BAN						
31-Jan-95	16:30	110	4.6			
26-Mar-95	15:30	160	7.5			
26-Apr-95	17:20	202	5.5			
30-Jun-95	17:10	188	7.5			
26-Jul-95	12:00	165	7.0			
15-Aug-95	09:30	156	5.0			
04-Sep-95	15:30	120	4.6			
09-Sep-95	15:30	76	3.0			
13-Sep-95	14:30	78	3.8			
17-Sep-95	13:00	60	2.0			
23-Sep-95	09:45	65	3.0			
27-Sep-95	17:30	70	2.8			
05-Oct-95	16:30		2.2	0		
15-Oct-95	08:30	77	3.4	0		
25-Oct-95	14:30	75	2.7	0	0.51	
05-Nov-95	09:30	81	2.8	0	0.35	
16-Dec-95	09:30	87	3.6	0	0.49	
20-Sep-98	17:30	83	1.3			0.38
23-Sep-98	10:20	64	1.4			0.01
01-Oct-98	07:45	64	1.0			0.01
08-Oct-98	07:45	68	1.0			0
14-Oct-98	06:00	71	0.80			0
23-Oct-98	16:45	60	0.90			0
29-Oct-98	06:15	60	2.4			0.01
07-Nov-98	08:00	37	0.80			0
28-Jan-00	15:30	46	0.74			0.11
01-Jul-00	15:15	89	1.3		0.24	0.16
12-Jul-00	07:00	92	1.1	4	0.73	0
13-Aug-00	16:30	80	2.1	3	0.30	
08-Sep-00	16:15	77	2.7	4	0.12	0.05

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (µg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
BEL						
28-Jan-95	14:45	130	5.0			
22-Feb-95	14:45	170	6.2			
19-Mar-95		162	5.0			
26-Apr-95	12:40	346	3.6			
13-May-95	11:00	134	6.0			
28-Jun-95	17:00	312	5.0			
14-Aug-95	10:30	104	7.0			
17-Sep-95	17:30	75	2.6			
07-Oct-95	08:30	76	3.3	0	1.3	
04-Nov-95	15:45	83	3.6	14	0.52	
12-Dec-95	17:10	86	6.0	8	0.37	
10-Jul-00	12:15	296	3.6	16	1.8	0.12
23-Aug-00	18:30	168	5.4	14	0.80	0.06
01-Sep-00	08:40	220	5.7	11	0.26	0.30
BON						
19-Jan-95	16:20	75	4.6			
26-Feb-95	12:00	90	4.6			
26-Mar-95		110	6.0			
30-Apr-95	10:40	120	5.0			
30-May-95	08:45	122	5.8			
30-Jul-95	17:00	88	3.0			
27-Aug-95	13:30	105	4.6			
24-Sep-95	13:40	60	2.0			
28-Oct-95	15:15	68	3.0			
26-Nov-95	12:00	87	3.3			
16-Feb-00	15:30	65	5.0	1		
22-Apr-00	11:00	78	1.0	1		0.06
21-Jul-00	16:00	83	1.0	1	0.19	
22-Jul-00	06:45	82	1.6	2	0.22	
05-Sep-00	09:20	62	1.8	4	0.12	
Budrock Pond, Anegada						
30-May-95	16:00	285	7.2			

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (μg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
FLA						
19-Jan-95	12:30	79	3.8			
26-Feb-95	13:30	92	3.0			
26-Mar-95	10:30	120	6.5			
29-Apr-95	14:50	159	7.0			
30-May-95	10:00	138	5.1			
31-Jul-95	17:00	110	4.6			
27-Aug-95	15:30	120	5.0			
24-Sep-95	11:30	65	2.8			
28-Oct-95	13:50	66	2.9	0	0.35	
26-Nov-95	13:00	81	4.1	14	0.24	
16-Feb-00	16:30	77	6.7	4		
20-Jul-00	17:00	126	3.4	4	0.26	0.13
21-Jul-00	05:45	108	2.7	3		0.11
04-Sep-00	15:00	70	2.3	7	1.2	
Great Harbour Pond						
18-Oct-98		34	0.40			0.01
Great Thatch Pond						
18-Oct-00		43	0.40			0.02
GUA						
13-Jan-95		74	3.3			
04-Feb-95	09:45	80	3.8			
18-Mar-95	15:15	79	2.8			
14-May-95	18:00	92	4.6			
23-Jul-95	16:30	120	4.6			
11-Aug-95	11:30	104	4.0			
23-Sep-95	15:00	43	1.2			
14-Oct-95	14:00	47	2.0	0		
19-Nov-95	11:30	43	1.6	0	0.30	
20-Sep-98	15:00	83	1.0			0.04
03-Oct-98	17:00	61	0.70			0.03
12-Oct-98	06:45	57	0.60			0.04
18-Oct-98	06:00	62	0.60			0.02

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (μg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
GUA (continued)						
25-Oct-98	17:45	41	0.60			0.01
29-Oct-98		40	1.0			0.01
10-Nov-98	07:00	28	0.90			0
01-Jul-00	11:30	84	2.8	2	0.18	
14-Jul-00	07:15	83	2.7	4	0.10	
14-Jul-00	15:30	83	2.2	1	0.19	
31-Jul-00	06:50	66	1.6	4	0.16	
JOS						
29-Jan-95	10:00	53	2.0			
20-Feb-95	09:00	86	3.3			
25-Mar-95	13:45	106	5.5			
13-May-95	13:45	38	1.8			
23-Sep-95	12:30	24	0.5			
07-Oct-95	11:00	27	0.4		0.13	
05-Nov-95	07:00	28	0.5	0	0.59	
16-Dec-95	12:00	35	1.0	12	0.42	
20-Sep-98	18:20	72	1.1			0.22
24-Sep-98	07:00	25	0.6			0.01
30-Sep-98	06:30	31	0.5			0.01
08-Oct-98	10:40	38	1.0			0.04
16-Oct-98	06:30	45	0.80			0.01
23-Oct-98	17:45	12	0.60			0.37
29-Oct-98	07:30	9	0.60			0.31
08-Nov-98		12	1.1			0.08
26-Jul-00	17:45	120	5.0	10	0.20	
24-Aug-00	16:00	32.2	1.3	9	0.34	0.25
LON						
19-Sep-98		130	1.6			0.06
23-Sep-98	15:50	43	1.1			0.01
29-Sep-98	06:15	48	0.90			0.01
07-Oct-98	06:15	60	1.7			0.04
13-Oct-98	06:00	63	1.0			0.02

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (μg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
LON (continued)						
23-Oct-98	17:45	50	0.80			0.01
29-Oct-98	17:45	40	0.80			0.02
08-Nov-98		40	1.0			0.01
Manhead Pond, Anegada						
16-Feb-00	15:00	97	2.6	0		
PTP						
20-Jan-95	09:00	75	2.8			
26-Feb-95	15:00	85	3.8			
26-Mar-95	0.733	67	2.8			
29-Apr-95	16:30	136	6.0			
30-May-95	11:30	136	5.5			
31-Jul-95	18:15	106	4.6			
27-Aug-95	16:15	120	4.8			
24-Sep-95	10:00	65	3.0			
28-Oct-95	17:00	46	1.1	0	0.80	
26-Nov-95	15:00	86	3.0	14	0.39	
16-Feb-00	13:30	48	2.3	1		
RED						
20-Jan-95	13:00	143	7.5			
26-Feb-95	10:30	212	7.0			
26-Mar-95	13:30	260	7.0			
30-Apr-95	09:45	255	7.0			
30-May-95	07:30	270	7.0			
30-Jul-95	15:20	180	6.0			
27-Aug-95	11:30	220	6.0			
20-Sep-95	15:00	72	2.6			
28-Oct-95	16:00	95	4.6	0		
26-Nov-95	10:45	130	5.0	16	1.1	
04-Sep-00	21:45	66	2.3	6	0.07	
SIN						
28-Apr-00	08:30	51	1.4	4		0.01
31-Aug-00	10:30	46	1.8	2	0.17	0.04

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Date	Time	Salinity	NO_3^--N (mg/L)	NO_2^--N (µg/L)	NH_3-N (mg/L)	PO_4^{3-} (mg/L)
SAL						
24-Jan-95	11:00	300	9.0			0
05-Feb-95	15:15	340	7.0			
05-Mar-95		273	7.5			
08-Apr-95		400	7.5			
08-Jun-95	14:00	400	7.7			
16-Aug-95	11:00	304	9.0			
27-Oct-95	14:03	220	5.0	0	1.3	
30-Nov-95	15:00	246	5.5			
WB						
29-Jan-95	17:00	38	1.4			
23-Feb-95	16:00	42	2.6			
19-Mar-95	16:45	65	3.6			
28-May-95	18:00	85	3.6			
07-Jul-95	10:40	67	4.0			
26-Jul-95	13:30	62	4.0			
15-Aug-95	14:00	60	2.6			
09-Sep-95	14:00	32	1.2			
07-Oct-95	12:30	27	1.4		0.39	
05-Nov-95	11:00	40	1.6	4	0.14	
16-Dec-95	14:00	53	1.8	0	0.64	

data in shaded cells were excluded from calculations of means (Section 3.3 (h))
blank cells represent cases where a parameter was not measured

Appendix D
Density of Mangrove Trees at Salt Ponds

	Number of trees per hectare of fringing forest				
	Buttonwood	White	Black	Red	**Total**
BAN	2546	0	0	292	2838
BEL	453	2471	0	1324	4247
BLU	467	257	9066	1125	10915
BON	3205	2470	16	1454	7146
FLA	1437	1575	2472	684	6168
GUA	0	15121	16	0	15137
HAN	2353	1985	662	221	5221
JOS	0	3128	6394	145	9667
LEE	2639	0	0	0	2639
LON	2341	463	3561	16	6382
NOR	0	4404	0	0	4404
RUN	831	4462	3077	1005	9374
SAL	0	0	0	0	0
SAN	1800	1400	0	0	3200
SIN	0	630	1815	8556	11000