

This is a slightly corrected version of the manuscript submitted and published in *Bahamas Journal of Science* 6:29–43. All but the most minor edits have been marked using WORD’s “track changes” facility.

## **Factors influencing the surface fauna of inland blue holes on South Andros, Bahamas**

**John M C HUTCHINSON**

School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK  
E-mail: John.Hutchinson@bristol.ac.uk

**Abstract:** We surveyed the macrofauna (particularly insects, molluscs and birds) of the surface waters of a series of inland, mostly anchialine, blue holes (flooded caves and associated lakes). The number of species was small, but the fauna varied considerably between holes. The following factors are evaluated as causes of these patterns: isolation and past inundation of Andros island, difficulty of dispersal between holes, topography (size of hole, water depth, whether ringed by cliffs), the surrounding vegetation, water quality (salinity, aeration, nutrients), tidal influence, human disturbance and pollution. Conservation issues are discussed, but generally the surface fauna is shared with far more extensive habitats on Andros. The same conclusion is drawn about the fauna of two subaerial caves associated with blue holes.

### **INTRODUCTION**

Blue holes are the entrances to flooded caves, occurring in the Bahamas both out at sea and inland. Cave diving has revealed a diverse and unusual fauna of crustaceans in these blue holes. For instance, a new class of Crustacea, the Remipedia, was first discovered in 1979 in a blue hole on Grand Bahama (Yager, 1981), and even within the last 12 years at least 20 new species of crustaceans have been described from inland blue holes. A phylogenetically related fauna is known from other islands on both sides of the Atlantic, and from the deep sea, but the level of endemism is considered high (Hart *et al.*, 1985; Stock, 1986, 1994). Given the limited samples available from such habitats, much remains to be discovered about the ecology and evolutionary history of this fauna, but few would ~~argue-disagree~~ that it gives the blue holes a high conservation value.

This rich endemic crustacean fauna is found at depth, remaining mostly in saline and anoxic waters. It is considered troglobitic and is distinct from the fauna found nearer the entrances to inland blue holes (Cunliffe, 1985; Stock, 1986). Much less attention has been given to the surface-water fauna, and even less to the partially aquatic fauna at the interface with the air. But since the deep-water fauna is fed by a detrital rain from the surface waters, the surface ecology can affect the deep-water ecology. Also any similar endemism in surface waters would strengthen the case for the conservation of the entire ecosystem. Accordingly in 1987 Paul Stewart and I surveyed the surface fauna of blue holes in South Andros as part of the interdisciplinary Andros Project. We studied only inland blue holes, and only from the surface. Our study should be viewed as preliminary; my intention is to provide hypotheses to test and a better idea of which animals to test them on.

This paper considers which factors might influence the composition of the surface fauna and why blue holes differ in their faunas. This also acts as a means to describe the surface environments of the holes systematically. Later I briefly discuss the fauna of two subaerial caves associated with blue holes, and then review the conservation issues. But first I describe the range of blue holes visited and the fauna sampled.

## SITES VISITED

During July and August 1987 we visited over 23 inland blue holes on South Andros, most more than once. Palmer *et al.* (1998b) describe each hole and their locations are given in Fig. 1. At about half of these we sampled the water surface, aquatic vegetation, and bottom sediment with a fine hand net, particularly looking for aquatic insects and molluscs. The time taken varied, partly depending on whether the bottom was within reach. Deliberate limitations of this study were that we rarely attempted to sample more than one metre underwater, we did not examine the microscopic fauna, and we noted only general aspects of the flora. We also did not attempt to sample at night, when some crustaceans and fish may emerge from hiding.

Conductivity measurements of surface water were made by Whitaker and Smart (1997a and pers. comm.). These have been converted to estimated salinities; local sea water has a salinity of 36 ppt, and water below 1 ppt is conventionally considered fresh.

The blue holes visited are divided into fracture-line and cenote types. The fracture-line blue holes occurred in two chains, the Bluff and Congo Town chains, both aligned along a linear fracture system running adjacent to the east coast. Evidence from salinity measurements, tidal changes, and cave-diving exploration indicates that the fracture-line holes are anchialine, connected underground to each other and ultimately to the sea (Whitaker and Smart, 1997a). In the Bluff chain the marine connection is at the southern end, so that salinity generally decreases northwards (range = 4.2–11.8 ppt; see Table 1). In the Congo Town chain the only known marine connection is to the north, and salinity generally decreases southwards; but all these holes are more saline than any of the Bluff chain (range = 12.9–25.9 ppt). The maximum explored depth of the fracture-line holes is ca. 100 m. The salinity at such depths is comparable with sea water, but the upper 15–25 m is brackish, the transition occurring at the halocline, a mixing zone under 10 m thick (Whitaker and Smart, 1997a, 1998). Along the fracture line the flooded vertical caves often adjoin shallower lakes, and I use the term “blue hole” to cover both.

Cenote blue holes are circular holes, typically 30 – 150 m across. They sometimes occur in small groups but otherwise are often several kilometres apart. On North Andros over 118 have been mapped (Little *et al.*, 1973); Smart (1984) compared their hydrology, and Proudlove (1984) made preliminary studies of their biology. On South Andros they occur in the interior, which is difficult to access. We visited two groups of cenote holes, one approached from Deep Creek (the Iguana Holes), the other from Little Creek. At each site two holes were examined. The Iguana Holes were visited three times, whereas the single visit to the Little Creek site was very hurried. The freshwater lens beneath the island makes the surface salinity of cenote holes low, except near the tidal creeks (3.3 ppt for the second Iguana Hole, but this tasted more saline than the other cenote holes; on North Andros the cenote holes typically had salinities under 5 ppt, and sometimes under 1 ppt— Smart, 1984). The vegetation and relief of the interior are also distinct from that along the fracture line, as discussed below.

For comparison we also visited various other aquatic habitats on the island. Fossil tidal creeks formed long shallow silted-up depressions with salinities of 4.9–8.7 ppt for two west of The Bluff Settlement, but of 25.6 ppt for one north of Congo Town fed by water from the Congo Town chain of fracture-line blue holes. Two small muddy potholes near Black Point

(NGR TB392567) had a low salinity (0.3 ppt) and a rich insect fauna, suggesting that they did not dry up seasonally. Also we carefully sampled several flooded quarries along the coast road. The water in these was rarely more than 1 m deep and their salinities ranged from 0.6 to 12.4 ppt. Another low-salinity habitat (2.7 ppt) was grassland between the coastal road and the raised line of palm trees, which after rain became flooded and, judging by the fauna of molluscs and amphibians, never dried out completely.

## THE FAUNA

We specifically searched for some taxa, whilst others were merely noted in passing. A general comment worth emphasis is that the macroinvertebrate fauna was not abundant and consisted of relatively few species. Proudlove (1984) also commented on the paucity of the fauna in the surface waters of blue holes on North Andros, as did Breder (1934) of the macroinvertebrates of large freshwater lakes in the interior of Andros. In contrast, the density of Crustacea in the halocline can be much higher (Palmer, 1985). Also much richer is the marine-like fauna and flora reported from the surface of more saline inland holes on Eastern Grand Bahama and San Salvador (Cunliffe, 1985; Godfrey *et al.* 1994).

### Coelenterata

A small pink hydromedusan (illustrated in Palmer, 1989) occurred in the southern holes of the Congo Town chain, at some sites in spectacular profusion. Based on observations in 1986 Palmer (Palmer *et al.*, 1998b) described the size range as 3–200 mm, but a size limit of 20 mm seemed more typical in 1987. It appears to be an undescribed species of *Ptychogena*, related to *P. crocea*, but this genus is not well studied (P.F.S. Cornelius, pers. comm.).

### Mollusca

The only bivalve found was *Polymesoda maritima*, abundant in sediment in the Congo Town chain, and in Mangrove Hole at the coastal end of the Bluff chain. Hydrobiid gastropods were abundant along the more saline holes in the Bluff chain (from Mangrove Hole to Nine Tasks Lake); those collected were *Littoridinops monroensis* and a species of *Heleobops*. The gastropod *Cerithidea costata* was found from Mangrove Hole to Donkey Hole, but also was widely distributed along the Congo Town chain. Rat Bat Lake and the waters in the associated cave were the only site where we found *Neritina clenchi* and *Neritina virginea*. We collected pulmonate freshwater gastropods (Physidae, Planorbidae, Ancyliidae, Succinidae) elsewhere on South Andros, but none in blue holes (see Pilsbury, 1930, for a species list from fresh and slightly brackish water on North Andros).

Molluscs are one group that has been thoroughly sampled in blue holes elsewhere in the Bahamas. Edwards *et al.* (unpublished) sampled quantitatively across three anchialine sites on San Salvador (salinities 20–26 ppt). The bivalves collected live were *P. maritima* and *Anomalocardia auberiana*; the gastropods were *C. costata*, *Batillaria minima*, *Cerithium minima* and *Melampus coffeus*. Four other mollusc species occurred dead in the sediment, and adjacent blue holes with a marine salinity had further species (Godfrey *et al.*, 1994). Cunliffe (1985) also listed other molluscs in Sagittarius, a saline (20 ppt at surface, 27 ppt at –2 m) anchialine cave and associated lake on Grand Bahama; *C. costata* was again present.

### Crustacea

No systematic collections were made. However, the conspicuous shrimp *Macrobrachium lucifugum* was common at the surface of School Hole, the most polluted site, but not seen elsewhere. Its habitat in other parts of the Caribbean is reported as caves and

anchialine sites (Hobbs, 1994), which does not suggest an association with pollution. A species of *Hyalella*, a genus of freshwater amphipods, occurred at least in Nine Tasks Lake and Battle Hole.

We noticed pelagic ostracods in several fracture-line holes, and dead ostracod carapaces formed much of the sediment in some holes. Ostracod assemblages from sediment cores in San Salvador blue holes are described by Crotty and Teeter (1984).

Land crabs are common throughout the coastal strip, so their presence around the fracture-line blue holes is unremarkable. However, in North Andros Farr and Palmer (1984) noted numerous land crabs at the base of blue-hole lakes 15 m underwater, so they could be important predators in this ecosystem.

### **Odonata (dragonflies and damselflies)**

A special study was made of this group. Around most holes we searched for exuviae, in some holes we found live nymphs, and we also noted whether adults were ovipositing. From this evidence at least seven species were breeding in blue holes: *Ischnura ramburi*, *Neoerythromma cultellatum*, *Anax junius*, *Brachymesia furcata*, *Erythrodiplax berenice*, *Macrodiplax balteata*, *Tramea onusta*. Table 1 shows the strong effect of salinity on diversity. *E. berenice* could breed even in the most saline holes, but the next two most tolerant species were not found breeding in salinities over 9.8 ppt. No dragonflies were observed around Swimming Hole and Co-op Hole despite each being visited twice in suitable conditions. The probable reason is that both lack shallows. The richest blue hole was Battle Hole (12 species), the least saline of the fracture-line holes, with extensive shallows, much algae and extensive overhanging vegetation. In comparison, several of the quarries filled with shallow fresh or weakly brackish water had 14 or 15 species frequenting them. In total we observed 26 species on South Andros, with indications of breeding for 16.

### **Heteroptera (bugs)**

Water striders were abundant on many blue holes. The following genera of aquatic bugs were collected, most only from Heron, School and Battle Holes, the least saline fracture-line holes sampled: *Limnogonus*, *Trepobates* (2 species), *Rheumatobates*, *Hydrometra*, *Buenoa*, *Pelocoris*, *Microvelia*, *Merragata*. In several species the adults collected were wingless and so must have bred on these holes. The fauna of non-blue-hole sites included extra species.

### **Coleoptera (beetles)**

We collected many species of aquatic beetle from such freshwater sites as quarries, but saw them in blue holes only four times: a diving species at Battle Hole, and small gyrids (whirligig beetles) on Swimming Hole, Nine Tasks Lake, and School Hole. Specimens from the latter site were of the genus *Gyrinus*, as were specimens collected from a rock pool alongside a cenote hole. In his paper on aquatic beetles of the Bahamas, Young (1953) remarks on a characteristic community of beetles found in brackish water, but this clearly did not occupy the blue holes that we visited.

### **Diptera (flies)**

Adult Nematocera (midges and mosquitoes) utilised in abundance the shade and still air afforded by the fracture-line blue holes, but we did not assess to what extent blue holes are used as breeding sites.

## Arachnida

We observed red water mites (Hydracarina) on the surface of several holes, as did Proudlove (1984) on blue holes in North Andros, and Breder (1934) on inland freshwater lakes. Two species were collected. There was also at least one species of spider walking on the surface of School Hole.

## Fish

Most holes contained small fish, but without a seine net we were able to sample only incompletely, and the collections made are unavailable at the time of writing. The greatest diversity of fish species was observed in the saline waters at the northern end of the Congo Town chain, and this fauna included larger forms, including a large eel. The most widespread fish were mosquitofish (*Gambusia*) and *Cyprinodon*. South Andros is the type locality of *Gambusia hubbsi*, where *G. manni* (another Bahamian endemic) is believed to be absent (Breder, 1934). Other authors lump both species into a single species, *G. manni* or *G. puncticulata*. *G. hubbsi* is the subject of ongoing evolutionary studies by Downhower *et al.* (1997) in the blue holes of North Andros.

On San Salvador Edwards *et al.* (unpublished) found that nearly all blue holes (salinities brackish or marine) had only the two species, *G. puncticulata* and *Cyprinodon variegatus*, with *Atherinomorus stipes* occurring in one inland blue hole of marine salinity. Breder (1934) discusses the fish fauna of large freshwater lakes in North and South Andros (12 species), and mentions finding *Haemulon sciurus*, *Lutjanus griseus* and *Lutjanus apodus* in a blue hole in the interior of South Andros (it is not clear whether this was in a creek). Proudlove (1984) also found *L. griseus* in two blue holes of salinities 1 and 3 ppt on North Andros. Both the crevice-living goby *Eliotris pisonis* and the blind cave fish *Lucifuga spelaeotes* are reported by divers to occur above the halocline as well as below (Palmer, 1998b).

## Amphibians and reptiles

We found no amphibians or reptiles in blue holes. However, tadpoles occurred in a rock pool in the karst beside a cenote hole.

## Birds

In our brief visits to the interior cenote holes, no birds were seen using them. Around the fracture-line blue holes we noted the following water birds. Common Gallinule (*Gallinula chlorups*) and Belted Kingfisher (*Megaceryle alcyon*): singletons, seen only at School Hole/Avalon and Battle Hole. Least Grebe (*Podiceps dominicus*): singletons, at Donkey and Gopher Holes. Green Heron (*Butorides virescens*) and Yellow-Crowned Night Heron (*Nyctanassa violacea*): widely distributed along both chains of holes, both seen at 8 holes each, but a total of 13 holes had one or other species, and usually several birds were present at each site; heron nests were present at Evelyn Green, Heron Hole, Battle Hole, Man Hole and Bolt Hole, but it was only at the latter where the Night Heron was definitely breeding. Extensive mangrove thickets must provide an abundance of other suitable aquatic habitat for these birds elsewhere on the island. See a later section for Cave Swallows and Barn Owls, two species utilising the caves and overhanging cliffs associated with the fracture-line blue holes.

## EXPLANATIONS OF THE PATTERN OF DIVERSITY

This section considers the physical and biological factors that could influence the fauna associated with a particular blue hole. Two general patterns in particular require

explanations—the general paucity of the fauna, and the considerable variation in the fauna from hole to hole. Examples of the latter include the apparent restriction of the shrimp *Macrobrachium lucifugum* to School Hole, the two *Neritina* gastropods to Rat Bat Lake, and the hydromedusan *Ptychogena* to a set of adjacent blue holes. Quantitative sampling would probably have revealed further differences: Edwards *et al.* (unpublished) studied molluscs from three adjacent and hydrologically very similar holes, where the relative abundances of species differed dramatically. Unfortunately many of the factors that might plausibly explain the faunal variation between holes covary, so it is not yet possible to draw definite conclusions about the main source of diversity.

## **Isolation and history**

### **(i) The general freshwater and brackish fauna of Andros**

Andros is an island and the blue holes are isolated habitats within this island, so one class of explanations for the species diversity considers the ease with which different taxa can colonise. These explanations depend not only on the biology of each taxa, but also on the current and past geography of the Bahamas archipelago.

Andros is the largest island of the Bahamas, although it is split by marine creeks into several smaller islands. Generally we expect that the larger the island the more likely that a species will have successfully colonised (MacArthur and Wilson, 1967). Andros' size also endows it with an extensive and thick freshwater lens and, in the interior, with large freshwater lakes (Breder, 1934).

South Andros is 200 km from Florida and 145 km from Cuba, which seems close enough for wind transport of arthropods as well as resistant stages of other small aquatic organisms. Although the prevailing winds in both summer and winter bring air from the empty Atlantic, air masses from the south are not uncommon and could transport biota from the Greater Antilles. But as important as current geography is the past history of the archipelago. From 120,000 years ago sea levels had fallen below current levels and 18,000 years ago were 130 m lower (Chappell and Shackleton, 1986). This created a much larger island, the Great Bahama Bank, the edge of which lay close to Cuba. This can explain why the Bahamian flora, much of the terrestrial fauna, and the non-marine fish fauna share more species with Cuba than with Florida (e.g. Browne *et al.*, 1993 and references therein; Rauchenberger, 1988).

A complication is the proposal that more recently (6000–4700 years ago) sea level may have been up to 4 m higher than today (Fairbridge, 1990). Biogeographic studies are broadly supportive of such an inundation (Browne and Peck, 1996), but it appears not to be widely accepted. Much more definitely established is that 125,000 years ago, during the last interglacial, sea levels were 6 m higher than today (Chappell and Shackleton, 1986). The cenote blue holes in the interior would then have been under the sea. The aeolian dune ridges along the east coast, through which the fracture-line caves run, are now up to 14 m above sea level (higher in North Andros) and would have survived the inundation, although the ecological conditions must then have been rather different. None of the Bluff chain of fracture-line holes (the chain now with less-saline water) occurs in land above the 6 m contour, and the islands left would be so narrow that drainage would drastically thin the fresh/brackish water lens. Permanent freshwater above ground quite probably disappeared. Black (cited in Breder, 1934) argued that the number of endemic freshwater molluscs described by Pilsbury (1930) from North Andros implied a great antiquity for this habitat on Andros, but the status of these taxa requires modern re-evaluation.

This probable extinction of most freshwater species (125,000 years ago if not 5,000) contrasts with the survival of the endemic crustaceans found at depth in more saline conditions. Stock (1986) points out that the Bahamas and Turks and Caicos have few low-salinity stygobiont endemics, whereas most of the Antilles have numerous such species. One

explanation is that any low-salinity endemics on low-lying islands such as Andros did not survive past sea-level rises. Perhaps surprisingly, the shallow water of anchialine ponds and blue holes seems generally not to have been recolonised by the halophilic stygo-adapted fauna found just below (Stock, 1986). Instead recolonisation could come either aerially from freshwater on Cuba and Florida or from species tolerant of marine salinities. The need for such recolonisation will bias which species are now available on South Andros to occupy blue holes, and could impoverish the total number of species.

Certainly tolerance of high salinities characterises much of the freshwater and brackish fauna. Breder (1934) considered that the fish living in the freshwater (1.5 ppt) lakes of Andros are “typically marine or at least brackish water” species. *Gambusia* can even be transferred directly between sea water and freshwater (Krumholz, 1963). More generally, Barnes (1989) argues that in all brackish faunas most species can tolerate full strength sea water, the exceptions being species derived from freshwater ancestors, which are never found in salinities over about 10 ppt. So, since blue holes with more saline surface waters would anyway be expected to have only species tolerant of sea water, and since such species could have survived on, or readily recolonised, Andros, we should not necessarily expect the fauna of these holes to be impoverished.

This need not be true of the less saline blue holes. The lack of fish restricted to freshwater is presumably because of the difficulties of colonisation. But our collections from other low-salinity habitats demonstrate that many species of insect and pulmonate mollusc restricted to low salinities have colonised or survived on South Andros.

I personally am unable to judge quantitatively how depauperate the blue hole fauna is compared with similar habitats in Cuba, Florida or Mexico. A similar question that others might aim to answer is whether blue holes on the other Bahamian islands have a poorer surface fauna than those on Andros, and whether this can be related to the islands’ size, distance from other islands, or height above sea level.

#### (ii) Dispersal between blue holes within Andros

Blue holes can be viewed as aquatic islands surrounded by dry land. But we need to consider the possible dispersal routes between blue holes to decide how isolated they really are. Difficulties of colonisation may restrict the distribution of some animals, but not that of animals able to use other dispersal routes. Very similar questions, concerning ease of dispersal and to what extent species composition is a matter of chance, have been asked about brackish lagoons in north-west Europe (Barnes, 1988).

Inter-hole dispersal will be particularly important if species periodically go extinct in some blue holes because of changes in sea level and water quality. Evidence for this kind of extinction in the last few thousand years is provided by Kjellmark (1996) for sediment-living bivalves and by Crotty and Teeter (1984) for ostracods. The probable reasons were climate-driven changes in salinity.

One possible dispersal route between holes is underground, since the fracture-line blue holes are connected by phreatic cave systems sometimes large enough to allow divers to connect separate entrances. Tidal flow along the fracture can transport material rapidly, but the rate is much slower in large diameter passage away from the sea (cf. dye tests in Cousteau and Diolé, 1973, and Whitaker and Smart, 1997a). Moreover, the connecting passages discovered between the South Andros fracture-line blue holes are beneath the halocline in saline water that mixes little with the overlying brackish water, at least in the Bluff chain. The high levels of hydrogen sulphide and low levels of oxygen in the halocline form an additional barrier. The fish *Lucifuga spelaeotes* and *Eliotris pisonis* occur both above and below the halocline (Palmer *et al.*, 1998a), but generally this seems an unpromising dispersal route for the surface faunas, even though much of it is tolerant of high salinities. In contrast, when sea

levels were lower in the Quaternary, the passages would sometimes have been at water level and could have acted as a highway.

In fact such a dispersal route within the freshwater/brackish lens probably still exists. Cores and the high permeabilities detected in pumping tests indicate that the limestone is permeated by interconnecting fissures up to a few centimetres across (Whitaker and Smart, 1997b). There is a fauna living permanently in this groundwater, some members of which may also utilise blue holes. For instance, the ostracod *Strandesia longula* is common in wells, pools, and the underflow of running waters in Haiti and the Bahamas (Broodbakker, 1984). Recently a live fish (probably *Lucifuga*) was pumped from a shallow well on New Providence Island, 4 km from the nearest blue hole (N. Sealey, pers. comm.). For such organisms even the geographically isolated cenote blue holes may be linked.

Underground dispersal might account for the increased diversity of fish observed in the northern holes of the Congo Town chain, the most northerly of which is only about 1.7 km from the marine connection at Driggs Hill Sinkhole. High surface salinities here suggest that the tidal flow is not so isolated from the surface water as in the Bluff chain, and thus that the underground route is more practicable. But their high salinities would anyway lead us to expect more marine fish, even if dispersal were not facilitated. The same factors may explain the highly diverse fauna of Sagittarius on Grand Bahama (Cunliffe, 1985) and of the saline blue holes of San Salvador (Godfrey *et al.*, 1994).

The alternative to the underground route between holes is overground. The fracture-line holes are often close to their neighbours, so that each can act as a stepping stone to the next. The cenote holes tend to occur either on their own or in isolated groups, but the low-lying honeycomb limestone in the interior can be covered with pits holding rainwater, and there are even large low-salinity lakes (1.5 ppt; Breder, 1934). At least on North Andros the narrower active creeks inland are also fresh (Smart, 1984). The freshwater “islands” are thus not so far apart, facilitating aerial dispersal. Rare floods may even provide an overground aquatic connection: storm surges associated with hurricanes cause large areas to be inundated with sea water.

An additional means of dispersal for fully aquatic organisms is in vegetation caught on birds’ feet. Shallow holes with overhanging vegetation are much more suitable for herons to feed and breed in, so ease of colonisation is one of several reasons why we might predict such holes to be richer. (But a test of such a hypothesis in isolated brackish lagoons in England did not show a relationship between faunal similarity and use by birds—Barnes, 1988.) In contrast some of the deep cenote holes of the interior, surrounded by treeless expanses of bare rock, seemed unattractive to bird life, and might thus be less liable to colonisation.

Perhaps there is an knock-on effect: once a hole has been colonised by one species of fish, herons are attracted and bring further aquatic life. More generally one could envisage that, following the last major extinction event driven by high sea levels (whether 120,000 or 5,000 years ago), blue holes showed a temporal succession driven by the slow colonisation of species, each of which could provide a niche for new colonists and cause the extinction of earlier colonists through predation or competition. An important open question is whether colonisation is sufficiently difficult, compared with the time since the development of the freshwater lens, that most blue holes are not yet saturated with species already present on Andros. Artificial introductions would settle the issue but ethically would be controversial. The following sections discuss several alternative explanations why different blue holes have different faunas.



## Topography

### (i) Size

The blue holes on Andros vary in size and shape. The cenote holes are circular with a typical width of 30–150 m, some being much larger. The fracture-line holes are more variable in shape, typically under 30 m wide and a little longer, but the length of the water surface may be up to 200 m (Nine Tasks Lake). Much of the organic input to blue holes must be from vegetation overhanging the holes, so large circular holes would tend to have relatively less. Larger holes are more exposed to winds, the effects of which are discussed below. Area may also be important in affecting the probability of colonisation and of chance extinction when population size is small (MacArthur and Wilson, 1967). The smallest populations are likely to be of the biggest animals, but the fish *Gambusia* and *Cyprinodon* often occur in abundance. However, fish predatory on these small fish, such as *Lutjanus griseus*, might quite plausibly be restricted to the larger holes. (Other predators high up the food chain, such as dragonflies, land crabs and birds can readily move between holes.) Also, commonly only small regions of each hole are shallow or vegetated enough to suit some species, whose populations consequently might be vulnerably small; total area of the hole would be a poor predictor of this.

### (ii) Shallows

Some cenote holes are deep shafts with vertical or overhanging walls continuing up to 100 m underground but much shallower cenote holes are common on North Andros (Proudlove, 1984). For instance, one cenote hole that we visited was nowhere deeper than 6 m deep, lined with a pale marl sediment. Many fracture-line holes also have extensive shallow lakes adjoining the deep shafts, and these holes tended to be faunistically richer, probably partly because they were richer in emergent vegetation.

In the shallows trees may grow, including the pond apple, *Annona glabra*, and mangroves at more saline sites. Many holes contained extensive areas of tall *Acrostichum* ferns, and smaller patches of sedges and rushes (the latter rather sparse). These plants provide shelter for surface-skimming arthropods and a source of organic input. In particular the emergent vegetation can recycle the nutrients locked up in sediment. Tree branches hanging low over the water are also where the herons nest.

Underwater much sediment in the fracture-line holes was overlain by mats of algae, which sometimes floated to the surface. In the cenote holes of North Andros Proudlove (1984) identified similar mats as consisting of blue-green algae; he emphasised their enormous bulk and ubiquity (lining much of the sloping walls and present in all but one hole). We often observed the damselfly *N. cultellatum* ovipositing on these floating floating mats. The algal mats provide food, oxygen, and shelter, but their consistency made searching for animals within them difficult. In some holes, such as Evelyn Green, the substrate was instead covered by calcareous algae, different colours mapping out concentric zones of a particular depth. In this and other holes extensive areas of soft pale sediment appeared bare of algae, and at least some of the cenote holes on South Andros appeared devoid of macroscopic algae. The microbial flora of the fully saline anchialine blue holes and hypersaline lakes on San Salvador sounds different again: Edwards (1996) describes “flocculent layers” of phytoplankton either lining the substrate or floating half a metre below the surface.

In Evelyn Green, the beds of calcareous algae are a likely source of the sediment, but the bivalve *P. maritima* living in the sediment also contributed noticeably. In other holes (e.g. Donkey Hole) the sediment was instead derived from hydrobiid snail shells and ostracod carapaces. These sediments provide a niche that in deeper holes is only present, if at all, on rock ledges around the vertical shaft (*P. maritima* did exist on narrow ledges in the otherwise deep Swimming Hole). If herons are to feed they will require at least such ledges to stand on.

In shallow holes dead organic matter remains potentially available to the ecosystem, whereas in deep holes it sinks down to float within the halocline, out of the range of surface dwellers. The shallower the water, the more likely that thermal convection, wind, and tidal disturbance can eliminate the stratification which loses the nutrients from the surface waters, and prevents oxygen reaching the sediment (see below).

Shallow parts of blue holes, if unshaded, felt noticeably warmer and no doubt show more diurnal fluctuations. Smart and Whitaker (pers. comm.) measured daytime surface-water temperatures in July 1986 at a range of holes. Although measurements were made at different times of day and on different days, a pattern seems to emerge. 33°C was the highest recorded, at School and Evelyn Green holes, which have extensive shallows. This compared with 29°C at the consistently deep but open Co-op Hole, and 26°C at Stargate (deep and overhung by cliffs). The water at depth was at 25°C. Temperature profiles at other deep holes in North Andros are given by Smart (1984), and their significance for stratification discussed below.

### (iii) Subaerial cliffs

Blue holes vary in whether the water surface is partly surrounded by subaerial cliffs. Cliffs several metres high are typical of most fracture-line blue holes, because these happen to occur along a line of lithified aeolian dunes. Nevertheless the shade was apparently insufficient to suit the rich fern flora associated in the Bahamas with the smaller “banana-hole” solution pits (Correll and Correll, 1982). The cenote holes of the interior lacked cliffs, as the water surface was only half a metre below the surrounding level plain.

Several cliffs around blue holes supported wasp nests and large Honey Bee colonies. The cliffs reduce wind at the surface, which should favour surface-skating insects, and clouds of mosquitoes, but also reduce aeration. Wind made the surface of the large exposed cenote holes quite choppy, and drove most dragonflies and damselflies away. In total contrast, Stargate Hole is small and partly overhung with cliffs, which must significantly reduce not only wind, variation in temperature, and light (factors that in open holes reduce stratification and/or increase aeration), but also reduce the input of wind-blown organic detritus. This is presumably why its waters are particularly clear.

### **Surrounding vegetation**

The fracture-line blue holes of South Andros occur along the coast, where the natural vegetation is a thick broad-leaved woodland or scrub. The proximity of the coastal villages has led to extensive clearing by burning, in order that crops like maize can be grown in the vacated solution holes. However, nearly all fracture-line holes still had trees around them. Tree leaves must be the major source into these holes of organic detritus, which supplies nutrients and affects the oxygen levels deeper underwater (see below). Woodland also reduces wind, and shields birds using the holes from casual disturbance from people working or walking nearby. In fact the woodland can be so impenetrable that holes away from cultivation are unlikely to be visited.

In contrast, some of the cenote holes in the unpopulated interior were in a flat rockland landscape, devoid of trees and very thinly vegetated otherwise, which accentuated their exposure to wind. The low detrital input into such holes may make them nutrient-poor, and thus explain their rather sterile appearance (pale blue in colour and lacking the algal mats found in many fracture-line holes, which looked distinctly greener and darker). Most of the blue holes examined by Proudlove (1984) in North Andros are cenote holes situated in forest, and they did have thick algal mats. Both cenote and fracture-line holes also occur in mangrove thickets.

Having noted that the surrounding vegetation could well affect the biology of the blue holes, one might equally ask whether the blue holes have any affect on the surrounding

vegetation, other than on those species already noted as growing in the water itself. Blue holes produce a permanent gap in the forest canopy, which seemed to enrich the epiphytic orchid and bromeliad flora in their immediate vicinity; but any such effect was minor, and unimportant given the frequency of artificial clearings.

## **Water quality**

### (i) Salinity

The surface salinity of the blue holes differed considerably, from 25.9 ppt (74% of sea water) to potably fresh (< 1 ppt), although the least saline fracture-line hole still had a salinity of 4.2 ppt. Brackish faunas world-wide are impoverished relative to those of adjacent fully marine or freshwater habitats, the minimum diversity occurring around 7 ppt (Barnes, 1989). Salinity is thus likely to be the major reason why the surface waters of the fracture-line blue holes, and of some cenote holes, contain few species. This is especially true of insects, which globally decline dramatically in diversity as salinity increases, and which showed this pattern strongly along the Bluff chain of fracture-line blue holes (Table 1). In contrast, the diversity of fish and molluscs declined as salinity decreased. It would be interesting to sample molluscs from further less-saline cenote holes, where perhaps diversity might increase again as strictly freshwater pulmonate species could colonise. Certainly the quarries and potholes with freshwater had freshwater pulmonates, as well as a dramatically increased diversity of insects.

Salinity varies not only between holes, but in blue holes elsewhere in the Bahamas can change in response to recent rainfall. Edwards *et al.* (unpublished) showed surface salinity in Watling's Blue Hole on San Salvador varying from 10 to 30 ppt at the surface and from 22 to 32 ppt deeper down (< 5 m). Heath and Palmer (1985) reported that at least 25 cm of almost potable water on the surface of the lakes in the Zodiac Caves on Grand Bahama disappeared within a month of no rain. However, rainfall is only sufficient to affect salinity much if rainwater is funnelled from a wider area. This is likely only where there is suitable relief, or adjacent to tidal creeks to which the lens drains (Whitaker, pers. comm.). On Andros the fresher and deeper freshwater/brackish lens means that irregularities in rainfall will matter less than on other islands.

A change in climate or a greater rate of water abstraction by man might lead to longer-term changes in salinity that could cause local extinctions. Crotty and Teeter (1984) took sediment cores from a blue hole on San Salvador and from three dramatic shifts in the ostracod fauna over the last 3,000 years interpreted considerable changes in salinity. Furthermore the shifts corresponded to salinity minima (Teeter and Quick, 1990). Four ostracod species showed only quantitative changes in abundance, but two species occurred only in the most saline zones. Kjellmark (1996) argued that the bivalve shells from a core in sediment currently 27 m underwater (15 m below the halocline) could only have been living there when these depths were oxygenated, perhaps because low rainfall led to the disappearance of the freshwater lens 3,000–1,500 years ago.

### (ii) Aeration and hydrogen sulphide

The smell of hydrogen sulphide ( $H_2S$ ) that divers notice at, and sometimes below, the halocline, and that is also apparent on disturbing sediment close to the surface, is a product of the anaerobic metabolism of organic detritus in these anoxic environments. Whereas the blue-hole endemic crustaceans are adapted to anoxic conditions, the surface fauna will be able to survive only in oxygenated water. In particular the surface of the sediment is likely to have a very different fauna depending on whether the water at that depth is anoxic.  $H_2S$  is itself highly poisonous, although it is not known how sensitive the surface fauna is to it.

In a 7 m-deep brackish blue hole Crotty and Teeter (1984) reported 5.4 ppm of oxygen at the surface, dropping to 2.4 ppm at –3 m (where the water was more saline), then dropping

suddenly again to 0.5 ppm at -5 m (where the water also contained H<sub>2</sub>S). At another blue hole Yager (1987) measured oxygen concentrations of 4 ppm near the surface, but below 0.1 ppm once the halocline was reached. Whitaker (1992) shows oxygen and sulphide profiles for some fracture-line holes on South Andros. The low oxygen concentrations are caused by oxidation of the organic detritus combined with a lack of mixing of surface layers. The low organic input to Stargate explains why its oxygen concentrations remain high to a great depth (H<sub>2</sub>S levels also do not rise). For more open blue holes the factors controlling the depth of aeration include the mixing effect of wind, tidal movements, and temperature changes. Solar heating of the surface layers will lead to a daily overturning when the topmost layers cool down overnight. Temperature profiles further suggest a yearly overturning to depths of several metres (Smart, 1984). (Although average temperatures in Bahamas show little seasonal variation, occasionally winter temperatures drop to under 10°C for 2–3 days and ice has been observed on one Andros blue hole—N. Sealey, pers. comm.) Nevertheless on South Andros oxygen levels can fall to low levels well above the halocline (Whitaker, 1992). The halocline prevents deeper mixing of surface waters, and in most holes accumulates organic matter that consumes the remaining oxygen and/or generates high concentrations of H<sub>2</sub>S. In blue holes too shallow for a halocline, organic detritus will instead accumulate on the bottom, where the depth of mixing will determine oxygen and H<sub>2</sub>S concentrations.

Near the surface another potential source of oxygenation is photosynthetic algae, either single-celled species in the plankton, or species forming floating mats, or benthic species such as the calcareous algae common in Evelyn Green and the encrusting mats of blue-green algae.

### (iii) Nutrients.

In both North and South Andros water clarity in most blue holes was excellent, which suggests that they contain few planktonic algae. K. Nelson (unpublished) confirmed that in several blue holes productivity in the water column was indeed very low, under 3 mg/m<sup>3</sup>/day. This is comparable with ultra-oligotrophic arctic lakes. Presumably the reason is a lack of one or more nutrients.

Since there is virtually no direct run-off into blue holes, input of nutrients must be limited and mostly be from fallen leaves. Conceivably at some holes the guano around heron nests may be a significant additional source. The surface water of many blue holes is stained dark, presumably owing to tannins. This implies that breakdown products of leaves enter the surface water, but other reasoning suggests that this is not so easy. In deep holes detritus sinks to the halocline, and be lost to the surface habitat. In shallower holes thermal stratification might similarly restrict nutrient availability. And even in the shallowest holes the sediment may lock up many of the nutrients. The strong smell of hydrogen sulphide when disturbing these sediments implies that bacterial breakdown is occurring without oxygen being able to get in, and thus probably without nutrients getting out. One bivalve was the only common burrowing animal in this sediment, so there is probably little mechanical disturbance that might help recycle nutrients, although wading herons might contribute. However, the *Acrostichum* ferns and flowering plants that grow into submerged sediment will be able to extract dissolved nutrients and make them reavailable, again mostly in the form of fallen leaves.

Proudlove (1984) observed that one hole in North Andros did have a rich plankton bloom. Comparing the nutrient concentrations in this hole with those in others would be the easiest clue to which are limiting. Phosphate is the limiting nutrient in most freshwater systems and is especially likely to be so in blue holes because carbonate is known to rapidly adsorb phosphate (Short *et al.*, 1985). In three fracture-line holes (Elvenholme, Stargate and Evelyn Green) phosphate concentrations throughout the water column are indeed low (below 0.1 mg l<sup>-1</sup>, the minimum detectability of the analysis kit—Whitaker, pers. comm.). Anoxic

conditions actually favour the release of phosphate, but if the surface of the sediment is not anoxic the high pH of the water will have the reverse effect (Payne, 1986).

### **Tidal disturbance**

In the fracture-line holes tidal movements are often obvious: even at the inland end of the Bluff chain tidal range is 0.3 m, half that of the sea (Whitaker and Smart, 1997a). On North Andros the tidal range of Ocean Hole was less (0.15 m; Farr and Palmer, 1984) despite being beside the sea, but even a cenote hole 18 km inland showed tidal fluctuations 6% those of the sea (Whitaker, 1992). In some fracture-line holes water streams in and out conspicuously from a shallow conduit in the wall. In other holes the inflow and outflow is imperceptible, and need not necessarily lead to much mixing if the underground connection is deep and spacious. But besides its effect on mixing and aeration, a tidal influence may restrict which animals can colonise. Barnes (1988) noted that the species restricted to brackish lagoons in north-west Europe are not found in other habitats not because they could not tolerate greater salinities, but because this is the only non-freshwater habitat lacking tides. As an example of the difficulties caused by tides for non-adapted organisms, we found young dragonfly nymphs left above water level during a low tide, and thus exposed to predation. And when dragonfly nymphs deliberately leave the water to emerge as adults, they risk being covered by a rising tide just when their new wings are drying. In contrast most plants growing as emergent vegetation probably are adapted to fluctuating water levels even if their normal habitat is not tidal.

### **Human Disturbance**

Palmer (1989) discovered that Sanctuary, a deep hole with a narrow entrance, had been used prehistorically by the Arawaks for human burial, and much more recently for the disposal of animal carcasses. This practice may have arisen simply as a solution to the difficulty of finding enough depth of soil to dig a grave, although the discovery of a canoe suggests that sometimes a ritual element was involved. Since some blue holes provide deep water-filled pits close to habitations, it is surprising that the only other South Andros blue hole where divers have noted rubbish is School Hole. Rubbish instead freely accumulates in the scrub behind each dwellings. Palmer (1989) commented that a sewage outfall also emptied into School Hole. In Sanctuary carcasses appeared to have been weighted, and would then sink well below the halocline. In School Hole some of the rubbish has settled nearer the surface; this and the sewage could influence the surface ecology, but there is no striking evidence of this, except perhaps for the poor visibility underwater.

In 1987 Nine Tasks Lake and the associated High Creek Caves seemed to be used extensively for laundry, whilst Katrina's Cave had been used for this purpose in the recent past. Palmer (Palmer *et al.*, 1998a) wondered whether this pollution was responsible for the absence of cave fauna at these sites. Blue holes are used because they provide less saline water that otherwise is not readily available. However, the water is still sufficiently saline that much soap is necessary, and bleach may be used to remove the smell of hydrogen sulphide. Regular laundry may also be a source of disturbance, preventing herons from nesting at some holes.

Holes are used for swimming by local children, but generally the sea is preferred. Indeed the local inhabitants view blue holes as rather sinister places. This may still be connected with the local mythology of the Lusca, an octopus-like creature that is believed to inhabit blue holes and drag down victims (Cousteau and Diolé, 1973). The halocline is too deep on Andros to be disturbed by non-divers, and bathers would be expected to avoid the soft stinking beds of sediment that are otherwise probably the habitat most sensitive to disturbance.

We saw no shotgun cartridges around any blue hole, although these were noted around a fossil tidal creek in the interior.

## THE DRY CAVES AND THEIR FAUNA

Many of the cliffs around blue holes overhang slightly, but at a few sites the overhang develops into a cave extending along the fracture. These caves are used as nest sites by two species of bird. In 1986 Cave Swallows (*Hirundo fulva*) were nesting in Twin Rifts Cave, the first breeding record for the Bahamas. No nests were in use there in 1987, but another two nests were found at Evelyn Green. The Barn Owl (*Tyto alba*) was observed around six of the fracture-line holes and disused nests were found on a shelf in one deep overhang. Of related interest are what were presumed to be nests of the extinct barn owl *Tyto pollens*, located underwater in a chamber beside Swimming Hole. The spoil included skulls of the hutia (*Geocapromys*), also now believed extinct on Andros.

We visited only two subaerial caves deep enough to have a dark zone. The larger is Rat Bat Cave, a passage connecting two blue holes (survey in Carew *et al.*, 1998). Except for one short section the passage is not constricted and continues some tens of metres, but much of this is lit by a diffuse light from the next hole. A much smaller cave was found along the fracture line just north of the north-east corner of Gopher Hole; it extends < 15 m along a moderately constricted rift.

Rat Bat Cave is so named because it contains a nursing colony of the bat *Erophylla sezekorni*, numbering in the order of a hundred. This nectar-feeding species is relatively common throughout the southern Bahamas and will roost in areas of caves where much daylight penetrates (Buden, 1976). Surprisingly little guano was found, which may imply that the colony is not very old, or just that it is used only for a short period of the year. Elsewhere in the Bahamas guano is assiduously collected from caves for manure (Campbell, 1978), which is a possibility here. The guano provides food for large numbers of the cockroach *Periplaneta americana* (now world-wide, but thought to be an introduction in America). Pitfall traps did not reveal further fauna in the guano. Also in this cave were the amblypygid *Paraphrynus viridiceps* and a cricket species of the genus *Amphiacusta*. This could be *A. bahamensis*, apparently endemic to Andros, but the specimens have not been compared with the type material. This was the only site where we saw a large boa (ca. 2 m long, presumably a species of *Epicrates*); it lay over the most constricted section of cave, possibly snatching bats flying through.

We visited the cave near Gopher Hole at dusk, when about six small bats flew in. However no bat guano was apparent. The fauna consisted of lots of *Amphiacusta* crickets (mostly around the entrance), amblypygids, a single small cockroach, spiders, two land crabs and two frogs under a boulder at the entrance. Such a fauna is probably typical of the many 1–2 m deep solution pits found in this area, offering cool and humid conditions. There was thus no evidence of the subaerial caves having any special fauna.

## CONSERVATION

The rather impoverished fauna associated with the surface waters of inland blue holes cannot add much to the conservation value of the fauna found at depth. The rate of endemism in the Bahamas is typically about 16% for terrestrial taxa (e.g. Browne *et al.*, 1993; Strohecker, 1953), so some of the fauna not identified to the species level may be endemic. But the freshwater fauna may be too recent, and the brackish water fauna not isolated enough, for their rate of endemism to be similarly high. A more important point is that the variety of other fresh and brackish water habitats on Andros mean that most species found in the surface waters of

blue holes are much more common elsewhere on the island. The shrimp *M. lucifugum* and the hydromedusan *Ptychogena* might be exceptions, but we cannot yet judge either whether these species are truly absent elsewhere on Andros, or whether there are other species restricted to surface waters of blue holes.

Other arguments for the conservation of the surface waters are currently stronger. (1) The undoubtedly valuable fauna found at depth relies on organic input from the surface layers and ultimately from the terrestrial vegetation surrounding the hole. Any toxic pollutants in the surface layers are liable to diffuse slowly downwards to the halocline. The biota of the surface waters may thus serve as an advance indicator of some threats to the deeper fauna. It may also serve as an indicator of changes to the water quality of the freshwater lens, which is a vital resource for the human population.

(2) The surface waters of the blue holes can serve as natural laboratories to answer general ecological and evolutionary questions. What makes them useful is that there are many isolated holes that can act as independent replicates, and rather few species. The environmental variation between holes that is stressed in this paper may or may not be an advantage. Currently at least two research teams are using the holes as natural laboratories (Downhower *et al.*, 1997; Edwards, 1996). Another scientifically valuable aspect of blue holes is that their sediments are stratified, thus preserving a record of past biota in sequence. Interpreting the climate that produced this biota is facilitated by the current environmental variation between holes (e.g. Teeter and Quick, 1990).

(3) The blue holes are aesthetically highly attractive, appearing as secluded oases ringed by shady cliffs in a landscape of hot sun, bare rock and thick woodland. There may even be a commercial value to preserving this beauty, since tourists and cave divers would be put off by holes full of rubbish or oil slicks.

Given that blue holes do have a conservation value, what are the threats to them? Potentially the most serious is the rise in sea level expected from global warming. Current estimates of the extent of sea-level rise have quite wide error bounds, but a 0.5 m rise by the year 2100 and a 1 m rise by 2200 are typical (Titius and Narayanan, 1996). Most of Andros is only a couple of metres above sea level, and even those holes not covered by sea are likely to be affected by a thinning of the freshwater lens and an increase in its salinity. The species most vulnerable are therefore those restricted to the surface waters of the least saline cenote holes.

Other potential threats may come from an increase in the human population, from a rise in the standard of living, and from industrial or tourist developments. The most serious consequence for blue holes may be pollution of the freshwater lens with sewage, salt water, or oil, and a thinning of the lens and an increase in its salinity through excessive extraction of freshwater. Such problems are documented by Edwards (1996) for San Salvador, and on the more developed islands water consumption has risen by 15% over 5 years (Whitaker and Smart, 1997b). Andros might seem less sensitive because it has a larger freshwater lens and the rather sparse human population is almost exclusively along the coast, but huge volumes of lens water are abstracted to be tanked to New Providence Island (Whitaker and Smart, 1997b). On Andros the increased provision of washing machines may increase water extraction and pollution of the freshwater lens generally, but the effect on the blue holes will probably be less than current laundry practises. Possibly with an increase in affluence agriculture and hunting will be practised less. Fortunately the Bahamas is free of malaria, but mosquitoes are a constant harassment, so attempts to control them by spraying open water near settlements is liable to affect the fracture-line blue holes.

More divers will visit the more accessible and spectacular of the blue holes. Deleterious consequences include disruption of the stratification and of the bacterial mats at the halocline (Palmer *et al.*, 1998a), enrichment of oxygen levels, and perhaps introductions of

fauna and flora. However, rather a small proportion of the holes are likely to be affected, and the publicity and revenue generated from tourists visiting these holes is probably a positive measure towards the conservation of others.

## CONCLUSIONS

This paper has demonstrated that individual inland blue holes differ considerably as physical environments. Consequently a diversity of factors could explain why their faunas differ. In the fracture-line holes I gauge that salinity and depth are the most important factors. In cenote holes the nature of the surrounding vegetation is likely also important. More rigorous answers will have to wait for more thorough sampling, but the presence of a large number of diverse blue holes in quite small an area will facilitate the disentangling of the various possible explanations. Indeed blue holes provide an excellent facility to further our understanding of brackish habitats generally.

## ACKNOWLEDGEMENTS

This paper is reprinted with minor modification, with permission, from *Cave and Karst Science* (the Transactions of the British Cave Research Association) Vol. 25(2), 83–81, August 1998. Fig. 1 is reproduced with permission from part of a figure in Whitaker, F.F. 1988, The blue holes of the Bahamas: an overview and introduction to the Andros Project, *Cave and Karst Science*, Vol. 25(2); thanks to Fiona Whitaker and Simon Godden for providing it.

Paul Stewart took an equal part in the often arduous field work on South Andros, and his experience benefited this work considerably. I thank the following experts for identifications (all specimens have been retained by their institutions): P.F.S. Cornelius, Natural History Museum, London (*Ptychogena*), F.G. Thompson, Florida Museum of Natural History (hydrobiids), K. Schniebs, Staatliches Museum für Tierkunde, Dresden (*Neritina*), R. Vonk, University of Amsterdam (*Hyalella*), C.H.J.M Fransen, Rijksmuseum van Natuurlijke Historie, Leiden (*Macrobrachium*), and J. Marshall, Natural History Museum, London (*Periplaneta* and *Amphiacusta*). Thanks to Fiona Whitaker and David Richards for their advice on the hydrology and sea-level changes, and to the former for providing unpublished data. I thank F. Whitaker, Graham Proudlove, Neil Sealey and Craig Edwards for their careful, constructive reading of the manuscript; the latter also supplied invaluable manuscripts of his own research. Joy Chaplain and N. Sealey provided hospitality in Nassau, and the numerous other contributors to the Andros Project are listed [in the \*Cave and Karst Science\* issue in which this article originally appeared elsewhere in this issue](#). All of the members of the Project generated a harmonious and stimulating working environment, but none of this would have been possible without Rob Palmer's drive and enthusiasm.

## REFERENCES

- Barnes, R S K, 1988. The faunas of land-locked lagoons: chance differences and the problems of dispersal. *Estuarine, Coastal and Shelf Science*, Vol. 26, 309–318.
- Barnes, R S K, 1989. What, if anything, is a brackish-water fauna? *Transactions of the Royal Society of Edinburgh: Earth Sciences*, Vol. 80, 235–240.



- Breder, C M Jr, 1934. Ecology of an oceanic fresh-water lake, Andros Island, Bahamas, with special reference to its fishes. *Zoologica*, Vol. 18, 57–88.
- Broodbakker, N W, 1984. The genus *Strandesia* and other Cypricerini (Crustacea, Ostracoda) in the West Indies. 2. Carapace length, ecology and distribution of two *Strandesia* species. *Bijdragen tot de dierkunde*, Vol. 54, 1–14.
- Browne, D J and Peck, S B, 1996. The long-horned beetles of south Florida (Cerambycidae: Coleoptera): biogeography and relationships with the Bahama Islands and Cuba. *Canadian Journal of Zoology*, Vol. 74, 2154–2169.
- Browne, D J, Peck, S B and Ivie, M A, 1993. The longhorn beetles (Coleoptera Cerambycidae) of the Bahama Islands with an analysis of species-area relationships, distribution patterns, origin of the fauna and an annotated species list. *Tropical Zoology*, Vol. 6, 27–53.
- Buden, D W, 1976. A review of the bats of the endemic West Indian genus *Erophylla*. *Proceedings of the Biological Society of Washington*, Vol. 89, 1–16.
- Campbell, D G, 1978. *The Ephemeral Islands: a Natural History of the Bahamas*. Macmillan, London
- Carew J L, Mylroie, J E and Schwabe, S J, 1998. The geology of South Andros Island: a reconnaissance report. *Cave and Karst Science*, Vol. 25, 59–72.
- Chappell, J and Shackleton, N J, 1986. Oxygen isotopes and sea level. *Nature*, Vol. 324, 137–140.
- Correll, D S and Correll, H B, 1982. *Flora of the Bahama Archipelago*. Cramer, Vaduz.
- Cousteau, J-Y and Diolé, P, 1973. *Galápagos—Titicaca—The Blue Holes: Three Adventures*. Cassell, London.
- Crotty, K J and Teeter, J W, 1984. Post Pleistocene salinity variations in a blue hole, San Salvador Island, Bahamas, as interpreted from the ostracode fauna. pp. 3–16 in Teeter, J W (ed.) *Proceedings of the Second Symposium on the Geology of the Bahamas*. CCFL Bahamian Field Station, San Salvador, Bahamas.
- Cunliffe, S, 1985. The flora and fauna of Sagittarius, an anchialine cave and lake in Grand Bahama. *Cave Science*, Vol. 12, 103–109.
- Downhower, J F, Brown, L P and Matsui, M L, 1997. Superfecundation: ecological constraints and rapid evolution. *Advances in Ethology*, Vol. 32, 468.
- Edwards, D C, 1996 The inland saline waters of the Bahamas as distinctive scientific resources. pp. 152–162 in Elliott, N B, Edwards, D C, and Godfrey, P J (eds) *Proceedings of the 6th Symposium on the Natural History of the Bahamas*. Bahamian Field Station, San Salvador, Bahamas.

Edwards, D C, Fregau, M R, Teeter, J W and Godfrey, P J, (unpublished). Molluscan assemblages and dominance relations in tidal, brackish inland blue holes, San Salvador Island, Bahamas.

Fairbridge, R W, 1990. The Holocene sea-level record in south Florida. pp. 427–435 in Gleason, P J (ed.) *Environments of South Florida: Present and Past*. Vol. II. Miami Geological Society, Coral Gables, Florida

Farr, M and Palmer, R, 1984. The blue holes: description and structure. *Cave Science*, Vol. 11, 9–22.

Godfrey, P J, Edwards, D C, Smith, R R and Davis, R L, 1994. *Natural History of Northeastern San Salvador Island: a “New World” where the New World Began*. Bahamian Field Station, San Salvador, Bahamas.

Hart, C W Jr, Manning, R B and Illife, T M, 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proceedings of the Biological Society of Washington*, Vol. 98, 288–292.

Heath, L M and Palmer, R J, 1985. Hydrological observations on the karst of Eastern Grand Bahama. *Cave Science*, Vol. 12, 99–101.

Hobbs, H H, 1994. Biogeography of subterranean decapods in North and Central America and the Caribbean region (Caridae, Astacidea, Brachyura). *Hydrobiologia*, Vol. 287, 95–104.

Kjellmark, E, 1996. Late Holocene climate change and human disturbance on Andros Island, Bahamas. *Journal of Paleolimnology*, Vol. 15, 133–145.

Krumholz, L A, 1963. Relationships between fertility, sex ratio, and exposure to predation in populations of the mosquitofish *Gambusia manni* Hubbs at Bimini, Bahamas. *Internationale Revue gesamten Hydrobiologie*, Vol. 48, 201–256.

Little, B G, Buckley, R V, Jeffries, A, Stark, J and Young, R N, 1973. *Land Resources of the Commonwealth of the Bahamas, Volume 4, Andros Island*. Unpublished Report for the Ministry of Overseas Development, Surbiton, England.

MacArthur, R H and Wilson, E O, 1967. *The Theory of Island Biogeography*. Princeton University Press.

Palmer, R J, 1985. *The Blue Holes of the Bahamas*. Jonathan Cape, London.

Palmer, R J, 1989. *Deep into Blue Holes*. Unwin Hyman, London.

Palmer, R J, Hutchinson, J M C, Schwabe, S J and Whitaker, F F, 1998a. Inventory of blue holes sites explored or visited on South Andros Island, Bahamas. *Cave and Karst Science*, Vol. 25(2), 97–102.

Palmer, R J, Picton, B, Stafford-Smith, M and Whiteside, D, 1988b. Brief reports of additional scientific investigations carried out during the Andros Project. *Cave and Karst Science*, Vol. 25, 103–104.

- Payne, A I, 1986. *The Ecology of Tropical Lakes and Rivers*. Wiley, Chichester.
- Pilsbury, H A, 1930. List of land and fresh water mollusks on Andros, Bahamas. *Proceedings of the Academy of Natural Sciences of Philadelphia*, Vol. 92, 297–302.
- Proudlove, G S, 1984. Preliminary observations on the biology of inland blue holes, Andros Island. *Cave Science*, Vol. 11, 53–56.
- Rauchenberger, M, 1988. Historical biogeography of poeciliid fishes in the Caribbean. *Systematic Zoology*, Vol. 37, 356–365.
- Short, F T, Davis, M W, Gibson, R A and Zimmerman, C F, 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine, Coastal and Shelf Science*, Vol. 20, 419–430.
- Smart, C C, 1984. The hydrology of the inland blue holes, Andros Island. *Cave Science*, Vol. 11, 23–29.
- Stock, J H, 1986. Two amphipod crustaceans of the genus *Bahadzia* from ‘blue holes’ in the Bahamas and some remarks on the origin of the insular stygofaunas of the Atlantic. *Journal of Natural History*, Vol. 20, 921–933.
- Stock, J H, 1994. Biogeographic synthesis of the insular groundwater faunas of the (sub)tropical Atlantic. *Hydrobiologia*, Vol. 287, 105–107.
- Strohecker, H F, 1953. The Gryllacrididae and Gryllidae of the Bahama Islands, British West Indies (Orthoptera). *American Museum Novitates*, No. 1618, 1–11.
- Teeter, J W and Quick, T J, 1990. Magnesium-salinity relation in the saline lake ostracode *Cyprideis americana*. *Geology*, Vol. 18, 220–222.
- Titius, J G and Narayanan, V, 1996. The risk of sea level rise. *Climatic Change*, Vol. 33, 151–212.
- Whitaker, F F, 1992. *Hydrology, Geochemistry and the Diagenesis of Modern Carbonate Platforms in the Bahamas*. Unpublished Ph.D. thesis, University of Bristol.
- Whitaker, F F and Smart, P L, 1997a. Groundwater circulation and geochemistry of a karstified bank-marginal fracture system, South Andros Island, Bahamas. *Journal of Hydrology*, Vol. 197, 293–315.
- Whitaker, F F and Smart, P L, 1997b. Hydrogeology of the Bahamian archipelago. pp. 183–216 in Vacher, H L, and Quinn, T (eds) *Geology and Hydrogeology of Carbonate Islands. Developments in Sedimentology*, Vol. 54.
- Whitaker, F F and Smart, P L, 1998. Hydrology, geochemistry and diagenesis of fracture blue holes, South Andros. *Cave and Karst Science*, Vol. 25, 75–82.

Yager, J, 1981. Remipedia, a new class of crustacean from a marine cave in the Bahamas. *Journal of Crustacean Biology*, Vol. 1, 328–333.

Yager, J, 1987. *Cyrtocorynetes haptodiscus*, new genus, new species, and *Speleonectes benjamini*, new species, of remiped crustaceans from anchialine caves in the Bahamas, West Indies, with remarks on distribution and ecology. *Proceedings of the Biological Society of Washington*, Vol. 100, 302–320.

Young, F N, 1953. The water beetles of the Bahama Islands, British West Indies (Coleoptera: Dytiscidae, Gyrinidae, Hydrochidae, Hydrophilidae). *American Museum Novitates*, No. 1616, 1–20.

Table 1. A list of blue holes where enough time was spent to estimate the dragonfly fauna. Holes are listed in order along each chain of holes, corresponding roughly to a decreasing salinity. An “s” in the third column indicates whether the sediment was searched for at least 30 minutes for submerged fauna. The next column gives the number of Odonata species observed flying around the blue hole or found as larvae. The other columns refer to the species *Erythrodiplax berenice*, *Brachymesia furcata*, *Neoerythromma cultellatum*, *Ischnura ramburi*, and *Libellula needhami*; the following letters are used as decreasingly certain indicators of breeding: A = nymphs or exuviae found, B = oviposition, c = mating, d = adult observed.

	surface salinity (ppt)	search	No. of species	<i>E. b.</i>	<i>B. f.</i>	<i>N. c.</i>	<i>I. r.</i>	<i>L. n.</i>
<u>Congo Town Chain</u>								
Lug Hole	24.9		1	A				
Man Hole	23.4		1	c				
Plug Hole	25.9		1	d				
Bolt Hole	21.6		1	B				
Hidey Hole	18.1		1	B				
Rat Bat Lake	12.9	s	4	A	d	d		
Swimming Hole	13.2	s	0					
<u>Bluff Chain</u>								
Mangrove Hole	9.8		5	d	A	A		
Evelyn Green	11.8	s	6	d	A	A		
Gopher Hole	9.3	s	4	B	A	A		
Donkey Hole		s	4	A	A	B		d
Nine Tasks/Round Lake	8.5		3	d	d	B		
Co-op Hole	5.1		0					
Heron Hole	4.2	s	4				A	
School Hole/Avalon	4.6	s	10	A	d	A	c	d
Battle Hole	4.2	s	12	A			A	
<u>Interior cenote</u>								
2nd Iguana Hole	3.3		5		A	A	c	d
1st Iguana Hole	< 1?		6		d		d	d

# FIGURES

Figure 1. Locations of the inland fracture-line blue holes along the east coast of South Andros, Bahamas.

