PROCEEDINGS

OF THE

THIRD JOINT SYMPOSIUM

ON THE

NATURAL HISTORY AND GEOLOGY OF THE BAHAMAS

Edited by

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San Salvador, The Bahamas

2023

3rd Joint Symposium
Gerace Research Centre
University of the Bahamas
on the Natural History and Geology of the Bahamas

LIFE & DEATH IN AN ANCHIALINE ARCHIPELAGO

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ABSTRACT

This report summarizes 20 years of natural history observation regarding animal diversity from 24 anchialine ponds on San Salvador Island and 16 ponds on the island of Eleuthera in the Bahamas, with special attention to the invertebrates. These ponds exhibit a wide range of species richness that appears correlated with their subterranean connectivity to the ocean. Greater species richness occurs in ponds with an intermediate degree of connectivity. Ponds with low connectivity become hypersaline or exhibit wildly fluctuating temperatures and salinity associated with storm events and periods of drought. Predictably, such ponds exhibit low invertebrate diversity. Ponds with high-volume subterranean conduits frequently support larger predators from the coastal environment access, and again, invertebrate diversity suffers. There appears to be a sweet spot with sufficient connectivity to permit the tidal fluxes that can buffer a pond against dramatic changes in temperature and salinity, while restricting access to larger predatory species. Anchialine ponds support species jackpots, where organisms, often rare on the open coast, undergo dramatic population expansions. Curiously, many species that successfully colonize the inland ponds exhibit various modes of clonal reproduction. The ponds themselves appear sensitive to dramatic environmental changes, both natural and manmade. The combination of restricted colonization followed by explosive population expansion within habitats that exhibit extreme physical and biotic characteristics makes the anchialine ponds a uniquely active evolutionary theater. After many visits, and stimulated by recent events in the world, I find myself compelled to close with reflections on our shared natural history ethos.

INTRODUCTION

Anchialine ponds (Gr. γχίαλος = "**near the sea**"; AN-key-ah-lin), (Stock *et al.*, 1986), include a wide range of inland salt-water habitats. In the Pacific, saltwater ponds have been well studied on the islands of Palau (Dawson and Hamner 2005; Dawson *et al.* 2009) and Hawaii (Seidel *et al.* 2016), but they have also been studied in the Mediterranean (Novosel *et al.* 2007), Bermuda (Stock *et al.* 1986; Thomas *et al.* 1992), and famously in the cenotes and underground water-ways of the Yucatan (Calderón-Gutiérrez et al. 2018). They are often associated with exotic life-assemblages, rapid evolutionary adaptation of their inhabitants, and almost inevitably they are faced with threats to their biotic integrity. Far less attention has been paid to the rich anchialine assemblage of the Bahamian archipelago.

Originally, anchialine ponds were defined as "*pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides*" (Holthuis 1973). This definition excludes salt ponds on the one hand, with no measurable connection to the sea, and lagoons with conspicuous coastal water connections. Other anchialine explorers have focused on the subterranean dimension of these habitats to the exclusion of their associated surface waters. Stock *et al.* (1986) defines them as "*bodies of haline waters usually with a restricted exposure to open air always with more or less extensive subterranean connections to the sea and showing noticeable marine as well as terrestrial influences*." Other authors even refer to them as "*underground estuaries*" (Bishop *et al.* 2015). The fact is, salt-water inland water bodies occur along a gradient of connectivity with the

sea: extreme isolation at one end of the spectrum and open lagoons on the other.

The Bahamian archipelago is rich in anchialine habitats that capture the full spectrum of ocean connectivity. San Salvador Island alone boasts 40 or more such ponds while Eleuthera has over 200. In the Bahamas, anchialine ponds have a variety of geologic origins effecting both their physical characteristics and their biotic diversity. Their origins are intimately associated with historic cycles of glaciation coupled with fluctuating sea levels (van Hengstum *et al.* 2019) and have been usefully characterized by Park *et al.* (2014). As sea levels rise, carbonate sand deposition leads to the creation and growth of wind-blown dunes and valleys (or "inter-dune swales"). Further sea-level elevation raises ground-water within the island's interior, ultimately breaching the bottoms of inter-dune swales and filling curvilinear lakes and ponds that hug the contours of the flanking, lithified dunes. These can be quite isolated from the ocean coast. Closer to the coast, lakes also form from lagoons that have been cut off from the ocean by sand deposition ("high-stand depressions", Park *et al.* 2014). Flooded inter-dune swales and cut-off lagoons are constructional lakes and ponds, forming as a consequence of sand deposition and rising sea level. Without a well-developed cavern connecting such lakes to the sea, and under regimens of low-rainfall and high evaporation, these ponds typically form hypersaline habitats, hostile to most forms of animal life. Destructional ponds form when processes of carbonate dissolution create voids in the subterranean island limestone that collapse, creating the famous blue holes. Dissolution processes can intersect constructional processes to create flooded inter-dune swales or cut-off lagoons with subterranean conduits permitting exchange with coastal waters. These processes have been vividly described by Carew & Mylroie (1994), Mylroie and Carew (1995), Mylroie and Mylroie (2007), and Mylroie (2019).

This gradient of connectivity determines both abiotic characteristics of a pond (salinity and temperature) and their biodiversity or community richness. Of particular interest to this study is the

invertebrate diversity. Satellite imagery can help identify ponds with a high likelihood of biotic richness. Ponds with marine salinities (frequently possessing subterranean conduits connecting them to the sea) appear blue in satellite imagery. Pea-green profiles indicate hypersaline lakes or ponds lacking zoetic diversity. Brown-black profiles typically imply brackish ponds with tannins from the surrounding mangrove or bush darkening the often-fresh surface-waters that can be layered over the denser saltwater forming a halocline. From field reconnaissance (24 lakes and ponds on San Salvador Island and 16 on the island of Eleuthera) it is evident that "blue" ponds have the greatest likelihood of complex invertebrate communities, but even among these, there are a few exceptionally rich ponds that deserve special attention, biodiversity sweet spots.

I offer a simple, straightforward model suggesting that invertebrate diversity within anchialine ponds is highest in ponds with an "intermediate" level of connectivity to the ocean. Too little connectivity and evaporation exceeds precipitation leading to hypersaline conditions that suppress invertebrate colonization and survival. Too much connectivity, either through conduits or overland during storm surge events, and large grazers and predators gain access to a pond where they contribute to predation pressures (much like on the open coast). Moderate connectivity supports colonization from coastal marine populations while suppressing predation. Organisms that are uncommon or even rare along the open coast often exhibit explosive population expansions in these inland refuges (population "jackpots"). Rising sea levels and increasingly severe storms have added to the dynamism of anchialine habitats, connecting or breaching formerly isolated ponds or subsequently severing connections with the sea through sand deposition. In this paper, I provide an overview of a brief (and very superficial) natural history survey of a variety of anchialine ponds on the islands of San Salvador and Eleuthera. It should be noted that many of the organisms found in these ponds are being studied in rich detail by other researchers with more tightly focused research aims. This paper addresses patterns of invertebrate diversity

within anchialine habitats in broad strokes, in particular drawing attention to five propositions:

1) Anchialine ponds serve as refugees, with "jackpots" of rare or uncommon species released from the predatory pressures encountered on the open coast.

2) Many organisms that have been successful anchialine colonists reproduce asexually or through some form of hermaphroditism or even parthenogenesis, life-history traits well-suited to colonization of these remote habitats.

3) There is a biodiversity "sweet spot" on the spectrum of connectivity that creates the richest invertebrate assemblage: too much connectivity and large grazers and predators are let in and ponds begin to resemble a heavily grazed lagoon; too little connectivity and colonization and species-diversity become restricted. In such cases, the abiotic system becomes sensitive to catastrophic weather-driven habitat change as there are no tides to mitigate a sudden influx of fresh, cold rainwater during a hurricane or buffer the system from excess evaporation during dry spells.

4) Anchialine habitats are dynamic, undergoing catastrophic change as well as slow motion editing and revision of community structure.

5) The same restrictions on migration that create a refuge for select marine organisms also promote their rapid evolutionary change.

METHODS AND MATERIALS

Ponds were identified using satellite imagery made available through Google Earth Pro. Underwater surveys were performed using mask, fins and snorkel in 24 ponds on San Salvador Island, and 16 ponds on the island of Eleuthera, (See Figures 1, 2, and Tables 1, 2). Surveys included multiple hours in each pond, often by several observers over multiple visits spanning two decades of research (less in the less populous or less biodiverse habitats), snorkeling with camera and specimen bags. Occasionally specimens were collected for close-up photography and identification back on land. Specimens were returned when practical, though

not when they appeared to have deteriorated. Temperature and salinity measurements were made using a hand-held Quanta probe. Images were captured using an Olympus TG5 underwater camera with housing and a Bluewater Photo 1000 lumen Focus light. Sun protection was achieved using neck-gaiter, booties, and full body skins (to avoid introduction of potentially toxic sun lotion or insect repellents).

RESULTS AND NATURAL HISTORY OBSERVATIONS

Anchialine ponds serve as refuges for marine invertebrates forming population "jackpots"

Release from coastal predation and interspecific competition ("ecological release", Kohn 1972) can result in dramatic population expansion of select species within the Bahamian ponds. Six Pack Pond on San Salvador Island (Figure 3) is non-tidal, lacks a conspicuous cave or conduit, and is over 3 km from the nearest coastline, yet Six Pack has a highly productive though species-poor marine community. It is nearly a perfect monoculture of *Batophora oerstedii* (a fuzzy finger algae). Unusually rich populations of *Batophora* and other Dasyclad algae have been noted in many anchialine habitats in the Bahamas (Woolbright *et al.* 2019). Molluscs present in Six Pack Pond include just three snails: *Battilaria minima*, *Cerithium lutosum* and *Cerithidea costata*, and five bivalves: *Polymesoda maritima*, *Anomalocardia auberiana*, *Isognomon alatus** (flat tree oyster), *Pinctada longisquamosa** (scaly pearl oyster) and *Brachidontes exustus** (the burnt mussel). This represents a classic euryhaline (salt-tolerant) molluscan assemblage (Teeter 1995), supplemented with a few mangrove prop-root species (marked with an asterisk) (Edwards *et al.* 1990). The dominance of this species assemblage in anchialine ponds is so iconic that it has been recognized as a marker for geologic habitat identification (the "*Anomalocardia auberiana* assemblage", Hagey & Mylroie 1995). Six Pack Pond also supports large populations of just two fish species, *Cyprinodon variegatus* (a pupfish) and *Gambusia spp.* (a mosquitofish).
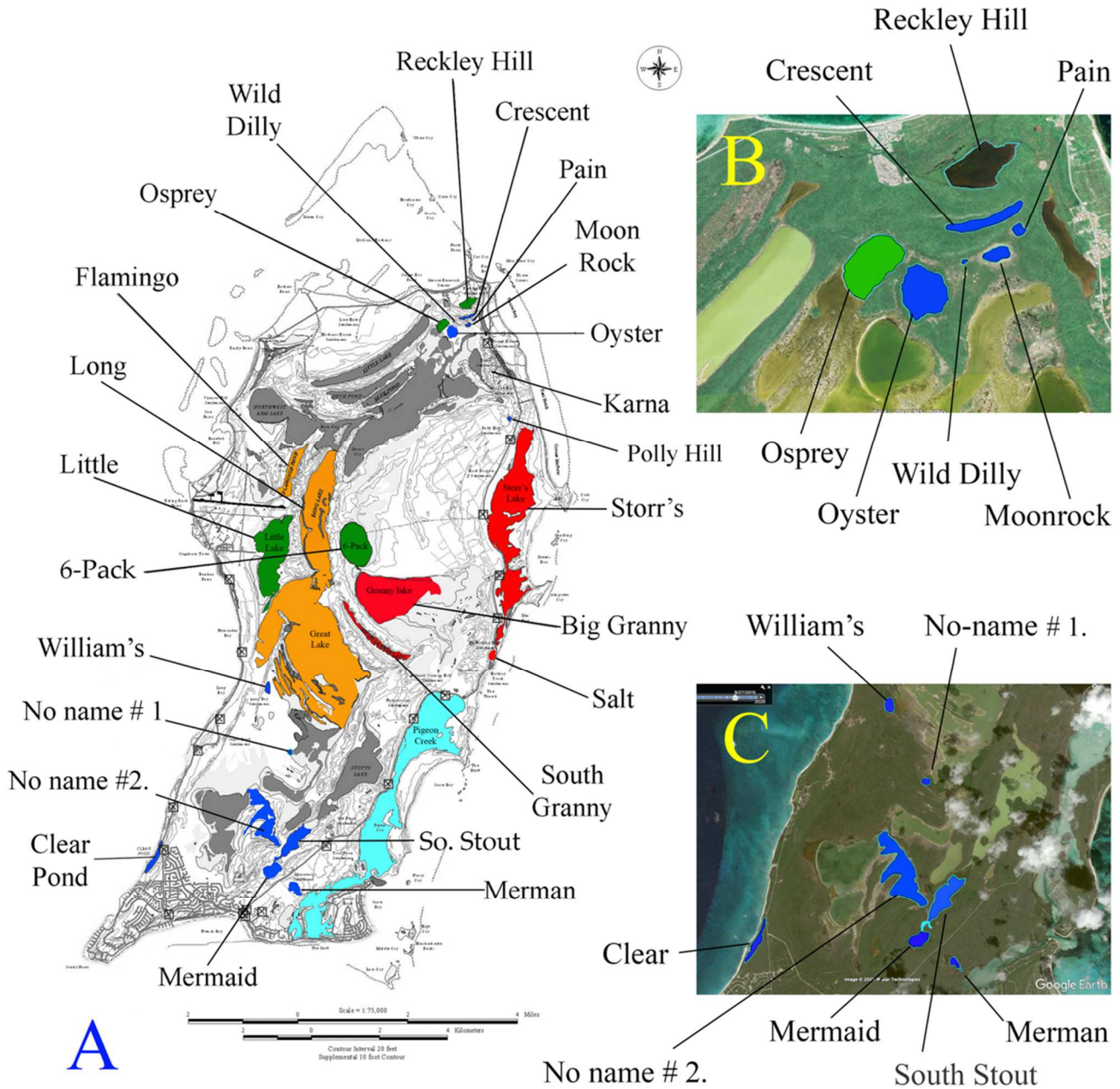
Figure 1. Twenty four lakes surveyed for animal diversity on San Salvador Island. Turquoise indicates lagoon with surface connection to the sea. Red indicates hypersaline (at times ≥ 80 TDS), orange: modestly hypersaline (TDS= 50-80 g/L), green saltier than ocean but habitable (40-50 g/L TDS), dark blue: fully marine (TDS 34-39 g/L). Asterisks indicate ponds of special interest. (A) Map is modified from one published by Robinson and Davis (1999), San Salvador Island GIS Database, University of New Haven and Gerace Research Centre. (B & C) Modified satellite images downloaded from Google Earth 7-11-2020, (images from 9/6/2019, 9/27/2015), Maxar Technologies. Preliminary physical characteristics and GPS coordinates appear in Table 1.
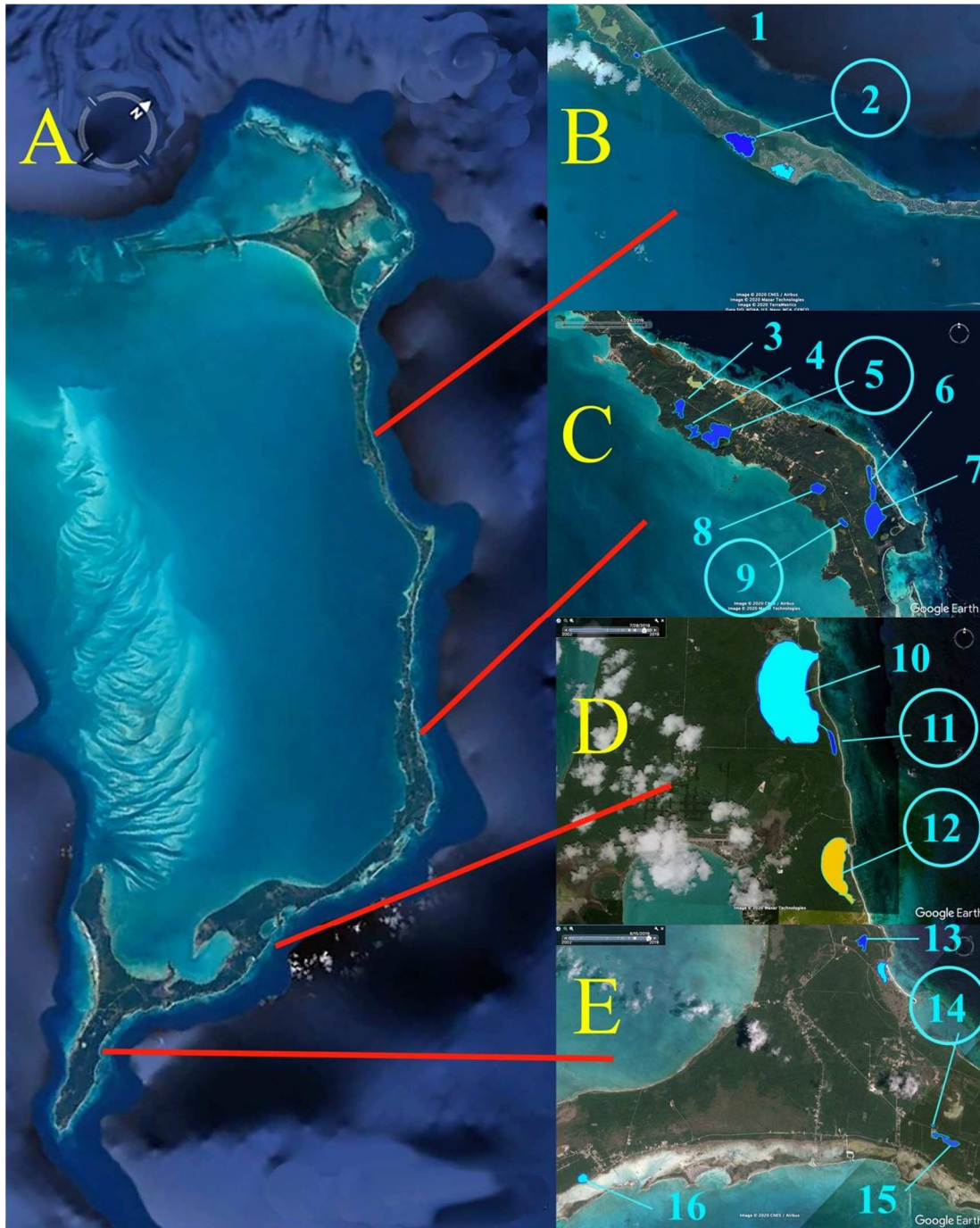
Figure 2. Sixteen anchialine ponds surveyed on the Bahamian island of Eleuthera. (A) This shows the entire island of Eleuthera. (B) This shows the northernmost ponds surveyed during our visits (note, there are more ponds further north!) (C) This indicates a rich collection of ponds just south of Governor's Harbor, (D) This map indicates ponds just north of Rock Sound, and (E) displays ponds on the far south end of the island. Circles specify ponds of special interest: (2) Sweeting's Pond, (5) Big Oyster Pond, (9) Un-named ("Synaptula") Pond, (11) Un-named ("Nurse-shark") Pond, (12) Red Pond and (14) Un-named ("Hawksbill") Pond. Ponds have been colored dark blue to indicate marine or near marine conditions (TDS ~ 35 g/L). Turquoise are fully marine lagoons with surface connections to the sea. Orange indicates ponds that were hypersaline at least sometime in recent history. Satellite images were modified from Google Earth images downloaded 7-11-2020, (9/6/2019, 9/27/2015), Landsat/ Copernicus, Maxar Technologies. Preliminary physical characteristics and GPS coordinates appear in Table 2.

Despite being species-poor, the organisms that have established themselves in Six Pack Pond (Figure 3) are remarkably dense. Virtually every frond of *Batophora* algae is decorated with a tiny sea grass anemone (*Bunodeopsis* sp.), a budding, nonsexual species that is well-adapted for clonal colonization. In 2006, a year and a half after Hurricanes Frances & Jean, juvenile scaly pearl oysters (*P. longisquamosa*) were found decorating the *Batophora* beds to a density of 250 individuals per square meter (Cole *et al.* 2006). This is in dramatic contrast to San Salvador's coastal sea grass habitat where, after 25 years, I have found only a single adult specimen of this *Pinctada*. It is probably no coincidence that this single specimen was located next to the outflow pipe of the GRC field station marine tanks where my research teams often held spawning adults collected from the inland ponds for study. We also found dense adult *Pinctada* populations in three of the larger (conduit-fed) ponds on Eleuthera (Great Oyster Pond, Little Oyster Pond, and Sweetings Pond). Six Pack Pond also provides refuge for a small, locally abundant hydromedusan jellyfish *Aquorea floridana* (Erdmann *et al.* 2009).

Figure 3. Six Pack Pond, San Salvador Island. From 12/2014. Google Earth, Landsat/ Copernicus, Maxar Technologies. Accessed 9-29-2019). Top left: image of shoreline from East trail entrance. Bottom left: characteristic <u>Batophora</u> monoculture during "peak" season with pupfish (<u>Cyprinodon variegatus</u>).

South of Edwin's Turtle Lake on Eleuthera (a popular tourist attraction), there is a less popular pond surrounded by a mature red mangrove forest. The bottom is covered in flocculent sediment with few conspicuous metazoans. *Rhizophora* prop-roots surrounding the pond support a calcareous green-algal garden that is the preferred real estate for two invertebrates: an opisthobranch gastropod (bubble snail, *Bulla sp.*) and a naked sea cucumber (*Synaptula hydriformis)* (Figures 4 A,B). This is the healthiest population of synaptids we have encountered from the Florida Keys, San Salvador, Eleuthera, and even Guadeloupe in the lesser Antilles where the species was first described by LeSueur (1824). *Synaptula* has a known affinity for calcareous algal outcrops (Jennifer Fricke and Richard Turner, personal communications), and the *Rhizophora* (mangrove) prop-roots of this pond

are uniquely rich in this particular habitat. It forms a *Synaptula* "Garden of Eden".

In another small pond on Eleuthera fed by a subterranean conduit, the cave shrimp, *Barbouria cubensis*, appear to have found a uniquely supportive refuge (Figure 4C). Without predation, this population also appears to have exploded.
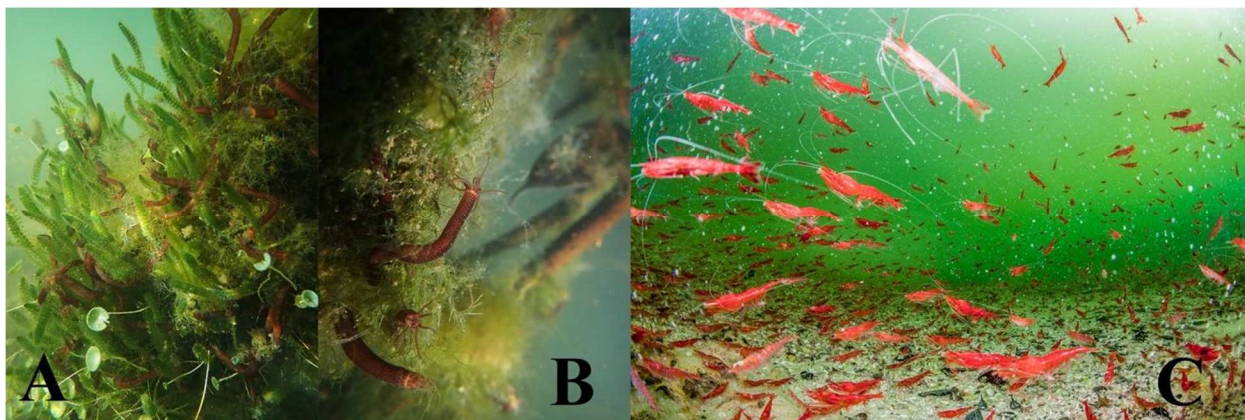

Figure 4. A, B, Brown synaptid sea cucumbers nestled in mixed green-algal masses adorning <u>Rhizophora mangle</u> (red mangrove) prop-roots. C. An impressive population of <u>Barbouria cubensis</u> in a small, conduit-fed pond on Eleuthera. Photo by Shane Gross. [https://www.shanegross.com/index.](https://www.shanegross.com/index)

An anchialine pond boasting extraordinary species jackpots is Sweetings Pond on Eleuthera. In 1985, Aronson and Harms (1985) counted 434 brittle stars, *Ophiothrix oerstedii*, per square meter on the pond floor compared with 3.2 individuals/m^2 from a nearby coastal site. Even a casual observer is impressed by the abundance of white nudibranchs grazing the algal gardens of Sweetings Pond (the fringe-back dondice, *Dondice occidentalis)* and brilliant red file clams (*Ctenoides scabra*) that are normally confined to under-sea ledges and rock crypts on the outer coast (Figures 5, A,B). In Sweetings Pond, file clams decorate carbonate outcrops in a way that seems highly exposed and conspicuous. There is also an impressive population of lined sea horses (*Hippocampus erectus*) that are extremely uncommon on the open coast (Figure 5C).

Figure 5. Three jackpot populations in Sweetings Pond: (A) The fringe-back dondice, (<u>Dondice occidentalis</u>); (B) File clams (<u>Ctenoides scabra</u>); (C) Lined sea horses (<u>Hippocampus erectus</u>).

Asexual, hermaphroditic, or parthenogenetic life histories favor successful colonization

For a species to become established in the more isolated anchialine habitats, it must overcome many of the same obstacles associated with island colonization. A single specimen of a sexually-reproducing species is unlikely to co-colonize with a partner permitting them to establish a breeding population. With regard to this point, it may be no accident that many organisms that have successfully colonized anchialine habitats are well-adapted for clonal colonization, reproducing as sequential hermaphrodites (*Pinctada longisquamosa,* the scaly pearl oyster), simultaneous hermaphrodites

(*Bulla sp*., the bubble snail), or even self-fertilizing, simultaneous hermaphrodites (*Synaptula hydriformis,* the naked sea cucumber and *Rivulus marmoratus*, the mangrove killifish). A single virgin individual from one of the latter species has the potential to establish an entire population within even the most isolated locations. The sea grass anemone (*Bunodeopsis* sp.) abundant in Six Pack Pond can reproduce by asexual budding. Closely related species have been shown to reproduce by shedding tentacles, even swallowing shed tentacles that regenerate and develop into entire polyps (Cutress 1979; Panikkar, 1937). *Aiptasia*, a rapidly reproducing anemone common to both Oyster Pond and Mermaid Pond on San Salvador Island (Mitchell 2017) as well as numerous ponds on Eleuthera, is capable of both sexual and asexual reproduction. A related species can bud off clones, each of which can subsequently develop into either male or female forms (Schlesinger *et al.* 2010). *Barbouria cubensis*, the red cave shrimp, may also be a protandric simultaneous hermaphrodite, though this has not yet been confirmed (Baeza *et al.* 2018). All these species exhibit reproductive strategies that make them especially adept as colonizing machines.

A gradient of connectivity with a "sweet spot" for invertebrate biodiversity

Ponds with low-connectivity. These include a great number of the flooded inter-dune swales and cut-off lagoons including South Granny and Storr's Lake on San Salvador Island and Red Pond on Eleuthera. Most ponds with little or no connectivity exhibit hypersaline environments inimical to all but the hardiest metazoan life (we have observed brine shrimp, *Artemia*, in Salt Pond on San Salvador Island). Storr's Lake is well known for the cyanobacterial mats and stromatolites that accrete in the hypersaline shallows. Six Pack Pond (described above for San Salvador Island) represents an enigma in that, while isolated from the ocean and exhibiting no measurable tidal displacement (two students camped along its shores monitored a tide-gauge for 16 consecutive hours… no tidal change), it maintains tolerable salinity (~40-45 PPT) and supports a species-poor yet highly productive community of marine organisms (see above). In brief, ponds with low connectivity typically exhibit species-poor invertebrate communities.
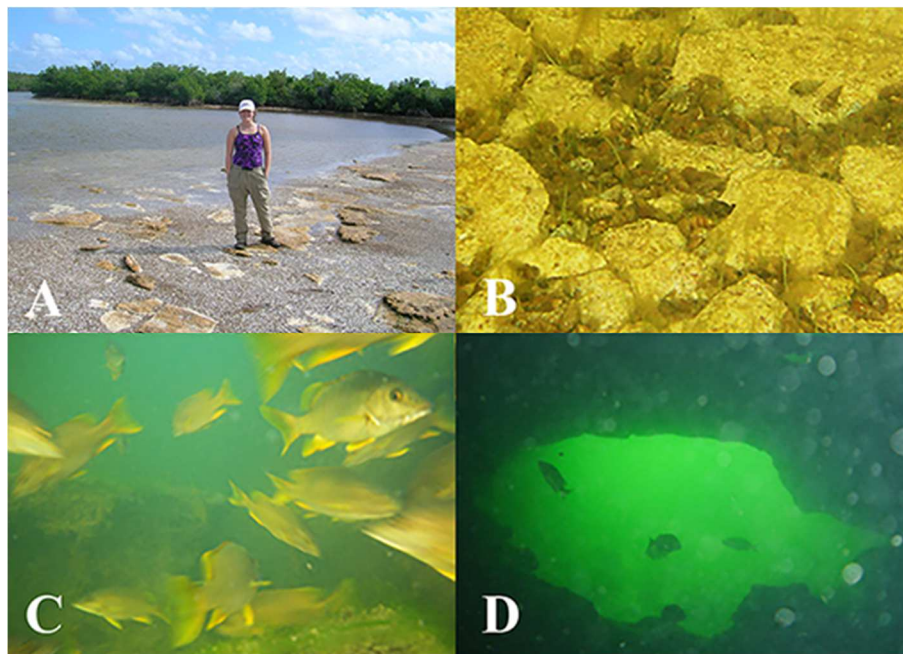

Figure 6. Merman Pond with co-discover, Keisha Sedlacek. (A) Shoreline with carbonate and shell hash. (B) Impoverished invertebrate community on carbonate bottom. (C) Schoolmasters at entrance to sinkhole. (D) Entrance to conduit from inside the cavern looking out.

Ponds with high-connectivity. Subterranean caverns linking inland ponds to the sea can serve as conduits for large predators and grazers. The consequence of increased connectivity can be observed in Merman Pond just east of Mermaid Pond on San Salvador Island (Figure 6). The shallow perimeter exhibits plenty of hard-carbonate substrate as well as flocculent sediments and, to the east, an abundance of *Rhizophora* prop-root habitat. The richness of habitat would lead one to anticipate a highly diverse invertebrate community. Infrared satellite imagery indicates that the pond remains cool. That said, the abundance of invertebrates is conspicuously low, including mostly members of the limited *Anomalocardia* assemblage described above. In the center of the pond is a substantial collapse feature with an impressive underwater cave entrance (2 m tall, 3 m wide). This sink-hole supports a rich population of large coastal reef fish including schoolmaster snappers (*Lutjanus cyanopterus)*, yellow mojarra (*Gerres cinereus)*, and crested gobies (*Lophogobius cyprinoides*) as well as American eels and, on one visit, a modest sized barracuda (White *et al*. 2007). The pond's margins support half-beaks (*Hemiramphus* spp.) and a tiny pipefish (*Syngnathu*s spp.).

American eels (*Anguilla rostrata*) are catadromous freshwater fish, migrating out to sea in order to breed and returning to freshwater between breeding seasons or to mature. Merman is a marine pond, occasionally and temporarily becoming brackish in response to large rainfall events, but returning to marine conditions as the conduit flushes its waters with daily tides. It is curious that adult eels appear content to accept Merman Pond (and 3 Roses Cave) as a freshwater habitat. (Juvenile eels have been collected from a freshwater marsh just south of the Gerace Research Centre on San Salvador Island). It seems likely that, despite Merman Pond affording excellent habitat, access to predators through its substantial conduit has significantly reduced its invertebrate diversity and abundance especially when compared with the rich invertebrate community only 600 meters away in neighboring Mermaid Pond. It may be significant that Merman Pond also exhibits a dramatic (>20 cm)

tidal flux with very little time lag, whereas Mermaid Pond exhibits a similar tidal flux that is substantially delayed (>90 minutes) from the coastal tide.

Ponds with moderate-connectivity (the sweet spot). Of more than 40 ponds on San Salvador Island, two exhibit unusually rich invertebrate communities (though others play a close second in terms of species richness). These are Oyster Pond and Mermaid Pond. What seems to characterize these sweet spots of invertebrate diversity is that both offer solid substrate for colonization (mangrove prop-roots and carbonate outcroppings rising out of the soft-sediments) and subterranean conduits with sufficient connectivity with the ocean to drive tidal changes (20 cm or more). Perhaps significantly, the tidal changes for both high-diversity ponds are substantially delayed with respect to coastal tides (1 hr 54 minutes for Oyster Pond, measured on Jan. 15, 2001, > 2 hr for Mermaid Pond), suggesting that, while exhibiting substantial tidal flux, they are none-the-less remote and/or restricted. In neither pond have we observed large predators or grazers from the coastal communities. In both ponds, the ubiquitous anchialine pupfish and mosquitofish are supplemented by schools of Atlantic silversides, *Menidia menidia*, observed during night snorkels around the conduits of Oyster Pond and even during the day in Mermaid Pond. Silversides might serve as an indicator species for moderate connectivity.

Nothing prepared us for the pond diversity on Eleuthera Island. After visiting only 16 ponds, my team encountered four sweet spots. Two of these have already received a lot of attention: Edwin's Turtle Lake (a popular tourist attraction) and Sweetings Pond (increasingly known for its striped sea horse population). The water body that attracted my attention was Great Oyster Pond, a relatively unvisited site south of Governor's Harbor and Edwin's Turtle Pond. This pond is tidal and possesses a rich variety of habitats from algal beds, sea grass flats, and soft-sediment (floc) bottoms to vertical carbonate outcrops. *Casseiopea* jellyfish are abundant, as are small fish (*Gambusia* and *Cyprinodon*) and a truly remarkable assemblage of marine invertebrates

Figure 7. Great Oyster Pond (A) Male <u>Cyprinodons</u> cruising algal beds. (B) <u>Casseiopea</u> jellyfish. (C) A biotic outcrop including urchins (<u>Lytechinus</u>) and an unidentified pink sponge. (D) A predatory tulip snail (<u>Fasciolaria tulipa</u>) prowling the Pinctada-laden <u>Thalassia</u> sea grass beds. (E) An anemone (<u>Aiptasia</u>) on red algal bed. (F) A species-rich assemblage of colorful marine sponges under a calcareous ledge. (G) High-density bed of scaly pearl oysters (<u>Pinctada longisquamosa</u>) on <u>Thalassia</u>.

Figure 8. (A) Three lagoons on Eleuthera Island. 1. An open lagoon; 2. Lagoon with restricted opening to sea; 3. Formerly cut-off pond with man-made channel connecting it to pond 2; 4. Cut-off lagoon with pea green profile (Red Pond). (B) A pair of breeding nurse sharks from tiny pond 3. (Dorsal fin of male "courter" can be seen at top left). Image from Google Earth, 2/27/02. Accessed 7/18/2020, Maxar Technologies. Couple mated minutes after this photograph was taken.

Figure 9. Red Pond on Eleuthera. Arrows indicate site of 2014 storm Damon wash-over. Note, change from pea green (hypersaline conditions) to marine blue. By 2019 image, beach was restored, and Red Pond is isolated. Images from Google Earth, Maxar Technologies.
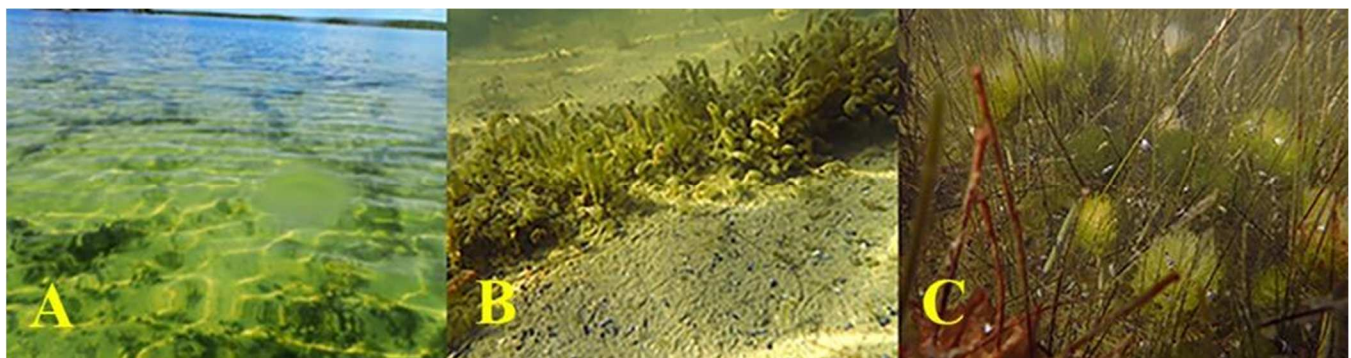

Figure 10. A, B), <u>Batophora</u> algae growing in Red Pond, anchored to large, polygonal, carbonate ridges surrounding patches of loose sediment. C) <u>Halodule</u> (sea grass) and <u>Penicillus</u> (algae) colonizing loose sediments, with small gastropod grazers.

including sponges, anemones, molluscs, and echinoderms (Figure 7).

Anchialine habitats are dynamic

We encountered several examples of anchialine ponds whose connectivity to the sea (or to other ponds) had been altered in recent history with dramatic consequences. Just north of Red Pond on Eleuthera (pond 4 in Figure 8), there is a coastal lagoon nearly cut off from the sea (pond 2). South of it (right) is a narrow pond that has been artificially connected to the larger lagoon via a 230-meter long channel cut by man into the karst (pond 3). It is almost certain that this narrow pond was originally isolated from the ocean by a substantial lithified dune and was likely hypersaline in character. A snorkel survey revealed that this pond has become a rich sanctuary for all kinds of reef fish and even green sea turtles. It had also been discovered by local nurse sharks, who have adopted it as a breeding site. Three adult sharks were observed over 2 short visits; two were mating along the shallow shore (Figure 8 B).

In this same cluster of lagoons, Google Earth images taken before December 2014 reveal that Red Pond (pond 4 in Figure 8A) is cut off from the sea, separated by a small dune with evidence of past wash-overs (Figure 9). The Google Earth image in Figure 8 matches that of a classic hypersaline pond. The pond's name (Red Pond) is consistent with the observation that, from shore, hypersaline ponds appear red due to the halophilic algae and microbes that populate the water column. Halophilic (salt-loving) algae and cyanobacteria change their pigment abundance from chlorophyll to carotene (green to red) in response to rising salt concentrations (Al-Hasan *et al.* 1987; Marshall 1982; Teeter 1995). Satellite images after this date reveal the waters of Red Pond to be blue and transparent, even revealing features of the pond bottom (Figure 9). It appears that the dune has been breached, re-connecting Red Pond to the sea. The catastrophic transformation of this hypersaline pond into an open lagoon has a precise date: Dec. 10, 2014. This was when tropical storm Damon struck

Eleuthera, nearly washing out the famous "glass bridge" on the north end of the island. It seems clear that this storm also breached the dune separating Red Pond from the sea, initiating a colonization event of a previously unpopulated pond.

In June, 2019 (five years after the hypersaline pond became a marine lagoon), we surveyed Red Pond by snorkel. Two things were remarkable. First, the pond had been colonized by coastal marine organisms. We encountered *Batophora* as well as *Halodule* seagrass and *Penicillus* (the latter two species NOT typical of a hypersaline environment). *Batophora*, which requires hard substrate to attach to, had formed polygonal tracks crisscrossing the soft sediment bottom (Figure 10A). Upon closer examination, the algae appeared to be anchored to raised, polygonal carbonate ridges. We suspect these polygonal tracks are relics of Red Pond's hypersaline past. Carbonate "megapolygons" have been associated with microbial mats in hypersaline, evaporation flats (Aref *et al.* 2014). They have also been described as arising from shallow intertidal or supratidal environments, as sediments follow cycles of desiccation, (creating polygonal cracks), wetting (causing expansion), and crystallization causing enlargement of the central platform and uplifting at the margins (Assereto and Kendall 1971, 1977).

Whatever their origin, these polygonal carbonate ridges form a solid substrate in Red Pond and have been colonized by the anchorage-dependent marine algae following the Damon inundation. The carbonate ridges are undercut and occupied by gobies (possibly *Lophogobius*). These small fish have excavated floc dens under the polygonal crusts. We observed larger schooling fish as well, though we were unable to identify them. Significantly, at the time of my visit, the surface connection between Red Pond and the sea had once again been blocked with sand. What had briefly been a lagoon was once again a pond (Figure 9). With evaporation exceeding precipitation, Red Pond is almost certainly on a return trajectory from marine to hypersaline conditions, with a concomitant extinction of its newly established residents. On a

larger time-scale, and with sea level rising, we are likely to see more of these cut-off lagoons breached and colonized in a similar fashion.

Evidence of a different slow-motion catastrophe can be found along the shores of Granny Pond on San Salvador Island (Figure 11). Most years, this large body of water is hypersaline (TDS = 80 g/L, Jan. 2006), and casual sampling has revealed little or no animal life. Paradoxically, the shoreline has a beach that is a half-meter deep in shell hash revealing that, at some time in its recent past, the pond was habitable. In January of 2009 following Hurricane Noel (Oct. 2008: little storm damage but 24 inches of rain), the salinity in Granny dropped from 80 to 49 g/L, well within tolerable limits for many anchialine organisms. The familiar red foamy waters had become clear, allowing us to snorkel and observe for the first time a rich stromatolite environment, a magnificent microbial crust, and a still sparse population of live gastropods.

Figure 11. A) "Granny Pond". B) Granny Pond's "shell hash" beach. C) Close-up of shell hash including gastropods and bivalves, machete blade for scale. (Google Earth, Maxar Technologies, GPS Coordinates: 24ᵒ 02' 38.61" N, 74ᵒ 29' 18.92" W, accessed 9/29/2019).

The deluge not only dropped the salinity of this big pond but connected it to its more productive and more stable neighbor 6-Pack Pond, allowing organisms to re-colonize and launching, no-doubt, another tragic cycle of colonization, isolation, and extinction.

These examples highlight the dynamic nature of anchialine ponds and their rapidly changing biota. Historic changes in pond connectivity are recorded in the fossil record as well (Hagey and Mylroie 1995; Teeter 1995; Park *et al.* 2009; Park 2012). As storms pass, connectivities change and newcomers are swift to colonize and exploit freshly available habitat. One can imagine a steady flow of organisms into anchialine habitats, with greater or lesser restriction to their immigration and, in some cases, almost seismic waves of death and extinction, grooming the community for the hardiest and best-adapted colonists. It is difficult to imagine a more forceful landscape for rapid evolutionary change.

Gradual change in organism assemblages within the Anchialine Ponds

I have described catastrophic changes that can occur in species composition in response to sudden changes in marine connectivity, both natural and man-made, but more subtle changes are taking place in species composition and community structure as well. When first published, the Field Guide to the Inland Ponds (Godfrey *et al.* 1993), described tunicates in both Crescent Pond and Oyster Pond on San Salvador Island. When I visited these ponds from 1995-2001 and surveyed organisms both along the shore and around the conduits, tunicates were not in evidence. I first believed that sponges had been mis-identified as tunicates, but having observed species turnovers throughout the years, it seems

possible that tunicates were present during these early surveys and were subsequently lost.

In Oyster Pond (San Salvador Island), I first observed beautiful serpulids (Christmas tree worms) decorating the red mangrove prop-roots in 1994. That was following an unusually long interval without hurricane activity. It has been 20 years since serpulids vanished from Oyster Pond. Some years, a species of sponge will become prominent, only to vanish or diminish again. In 2008, I noticed that the prop-roots in Mermaid Pond, where I had formerly collected oysters, were supporting a species of red algae from the *Laurencia* complex (possibly *Palisada poiteaui*). What began as a modest incursion exploded over the next two years, until I could no longer find my oysters. They had disappeared under bushels of the red algal over-growth. I rediscovered them only by burrowing through armfuls of the stuff to expose the *Rhizophora* prop-root where they remained stubbornly anchored. In later years, though the *Laurencia* persisted, oysters appeared to migrate to the periphery of the red-algal shrouds, where they once again could filter planktonic algae from the water column unobstructed. It is a cautionary tale that visitors to the ponds may not be observing a definitive stable community of organisms, but a snapshot of a community that is almost certainly in flux.

Rapid evolutionary change

The conditions that have created anchialine sweet spots, excellent habitat and limited connectivity to the sea, also create conditions that favor rapid evolutionary change: limited gene flow and founder-effect genetic bottlenecks. Individual ponds exhibit profoundly different physical characteristics while providing widely divergent selection pressures on subpopulations of the same species.

In one example, scaly pearl oysters (*Pinctada longisquamosa*) are relatively uncommon in most of the inland ponds. I have observed live populations in only six ponds on San Salvador Island and two ponds on Eleuthera. By contrast, they are richly abundant in sea grass beds on the Gulf side of the Florida Keys. On San

Salvador Island, the *Pinctada* from Oyster Pond and Six Pack Pond are markedly different despite being separated by only 6 kilometers. Oysters from both Oyster and Mermaid Ponds have elaborate scales (Figure 12 A). Oysters from Six Pack Pond are smooth-shelled, with greatly reduced scales (Figure 12B). There also appear to be differences in frequency of pigment stripes on the shell and soft-tissue pigments (Cole *et al.* 2016). The most impressive difference between these populations is in their reproductive life histories. Oyster Pond *Pinctada* populations (as with most wild populations) exhibit protandrous hermaphroditism. They begin their reproductive lives male and switch unidirectionally to female (Cole *et al.* 2010, Halvorson *et al.* 2012). Oysters from Six Pack Pond, on the other hand, exhibit bidirectional sex determination. Large adults from Oyster Pond are almost exclusively female, while those from Six Pack Pond are 50:50 male and female.
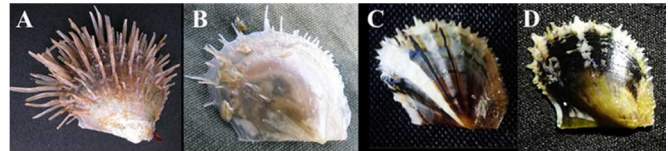

Figure 12*. Phenotypic variation among scaly pearl oysters (*Pinctada longisquamosa*) photographed from different islands, and from different ponds on the same island. A) Mermaid and B) Six Pack Ponds (San Salvador Island), C) Great Oyster Pond and D) Sweetings Pond (Eleuthera).*

Evolutionary changes in *Pinctada* characteristics appear between island populations as well as between isolated ponds on a given island. The oysters from Great Oyster Pond on Eleuthera have developed a rich suite of shell pigments never seen in the San Salvador populations. Sweetings Pond oysters, while also richly pigmented, are distinct from Great Oyster Pond oysters in that their pigments show greater shell coverage, while Great Oyster Pond oyster pigments are more restricted to delicate bands and stripes (compare Figures 12 C & D).

There are a great many examples of rapid evolutionary changes in populations from different ponds and different islands in the Bahamas. The fact that these ponds have only become ponds since the last Ice Age reminds us

that the habitats themselves are less than 10,000 years old. Consequently, changes in the phenotypic characters within neighboring pond populations have almost certainly emerged on a similar, rapid timeline.

Anchialine Commuters?

During a snorkel survey of a small, *Batophora*-rich pond on the south side of Eleuthera, my team and I discovered a juvenile hawksbill turtle (*Eretmochelys imbricate)* perched 15-20 feet down on the ledge of a massive underwater cavern (Figure 13). This pond clearly had a destructional origin through karst dissolution and collapse. The hawksbill may have been captive for some time in that the trailing edge of its carapace had mature *Batophora* algae growing along its margin.

Figure 13. A) Hawksbill turtle perched near sink-hole/conduit feature in a small pond on south Eleuthera. (Batophora is growing off posterior margin of shell). B) Turtle after capture and before release. C) First encounter between our camera-mounted juvenile hawksbill and an aggressive green sea turtle off of Powell Point, Cape Eleuthera. (See video: https://youtu.be/xkEZ_pA7580). Photo credits to Nathan J. Robinson, Cape Eleuthera Institute.

Dr. Nathan Robinson of the Cape Eleuthera Institute assisted us in capturing the turtle, and tissue samples were taken. We then transported the hawksbill to the Cape Eleuthera Institute, where we secured a video camera with a time-release fastening onto the carapace, and released the turtle into a nearby harbor. The camera was recovered hours later, and we were able to witness the hawksbill's encounter with a native green turtle out on the reef. Finding a hawksbill in a tiny, inland pond over a kilometer from the ocean was somewhat mystifying. Islanders have introduced sea turtles to some of the inland ponds as tourist attractions (see Edwin's Turtle Lake) and historically as a source of food (Carew and Mylroie 1994). That said, this particular pond seemed an odd choice as it holds no tourist appeal and appears to be a difficult place to retrieve a turtle from. (The conduit was easily 10 m deep before tapering). The other possibility is that this turtle actually navigated the large submarine conduit from open coastal waters (over a kilometer away). This unlikely possibility

is given credibility by a second hawksbill encounter in Clear Pond on San Salvador Island.

Clear Pond is a classic cut-off lagoon. The pond is only a few hundred meters from the ocean and cut off from the sea by a narrow dune. The landward shoreline abuts the Queen's Highway and a gently rising hillside. Despite being a classic constructional, high-stand depression or cut-off lagoon, there is a conduit on the landward side of the pond (Dalman 2009). Possession of a conduit reflects destructional processes at work as well (carbonate dissolution). This highlights the complex intersection of geologic and hydrologic processes at work on the islands. The water issuing from this opening, which paradoxically abuts the inland shore not the seaward side, seemed brackish, suggesting that the cavern may open onto the freshwater lens beneath the inland hillside. Milling about in the scour created by the rather forceful current from this conduit were snappers and other lagoon fish. Previous researchers even reported a barracuda (Dalman 2009). Perched under an overhanging rock was yet another, this time full-grown, hawksbill turtle

(6/11/2019). This pond, which is shallow (maximum depth < 1M) and actually "hot" to the touch (35°C), seems an unlikely place for an islander to cache a purloined sea turtle. Furthermore, upon my return, the turtle had vanished. We were convinced it had re-entered the cave system. Snorkeling into the cavern's entrance, we found the walls thickly covered with marine sponges, nearly 20 cm deep in places, preferred food for hawksbill sea turtles. We must at least entertain the notion that sea turtles are capable of traversing some of the larger submarine conduits emerging inside an anchialine pond, and may actually do so at will.

DISCUSSION

A Goldilocks scenario drives invertebrate community richness

Surveys of 40 ponds on the islands of San Salvador and Eleuthera in the Bahamas reveal that Google Earth imagery can be used to identify habitats potentially rich in invertebrate bio-diversity. Ponds with weak or nonexistent connectivity to the sea tend to be predictably low in zoological diversity. Ponds with strong ocean connections exhibit only modest biodiversity reflecting, we suspect, higher predation and grazing from typical lagoon or reef denizens. Ponds with only moderate connectivity exhibit the sweet spot for biodiversity, a "Goldilocks" scenario.

Anchialine ponds are refuges for marine diversity, a call for conservation

Ecological release (absence of predators or competitors) allows the rare colonist to undergo a population explosion creating jackpots of often uncommon coastal species. This raises two issues. First, these population jackpots represent a natural refuge for select coastal organisms, making them high-profile targets for vigorous conservation efforts. Second, given the general decline of coastal marine communities, these pockets of organismal diversity may actually be capable of supporting a kind of reverse colonization (Bellemain and Ricklefs 2008).

Attention is typically paid towards how an island habitat becomes colonized. Less attention is paid to the possible emigration of organisms from an "island" to the "mainland" (in this case the "island" is the anchialine pond, and the "mainland" is the open coast). This provides a spotlight on why these habitats should receive urgent protection.

Engines of evolutionary change (islands within islands)

Islands have long been celebrated for their role in accelerating evolutionary change, and for bringing about conspicuous, rapid species radiation (MacArthur & Wilson 1963, 1967). The Bahamas have served up numerous case-histories of rapid species diversification and endemism among their terrestrial inhabitants: *Anolis* (Losos 1990; Mahler *et al.* 2013), *Cerion* (Goodfriend & Gould 1996; Harasewych & Tenorio 2018), and *Cyclura* (Schwartz *et al.* 1977; Richardson *et al.* 2019) as well as among the island's anchialine inhabitants: *Cyprinodons* (Martin & Wainwright,2013; Turner *et al.* 2008), *Gambusia* (Martin *et al.* 2013; Fowler *et al.* 2018), and *Hippocampus* (Masonjones 2019; Rose *et al.* 2016). To this growing list we can now add *Pinctada longisquamosa*, the scaly pearl oyster, whose soft-tissue pigment, shell anatomy and coloration, as well as life-history characteristics have seemingly adapted to variations in individual pond environments (Cole *et al.* 2010, Halvorson *et al.* 2012).

A NATURAL HISTORY ETHOS.

Ethos: the characteristic spirit of a culture, era, or community as manifested in its beliefs and aspirations. During these investigations, I've grown increasingly aware of my own impact on these extraordinary natural habitats. In penance, I'd like to draw attention to an *Ethos* that the many good naturalists who have come before have tried to transmit, and which I have imperfectly emulated in my own work. We don't often think about or discuss these issues with one another or with our students who are

acutely tuned to the tenor of our relationship with nature. For future generations:

Leave behind the sun lotion. We can cover ourselves head to foot with long-sleeved clothing (or a light-weight snorkel skin), and purchase a light-weight flexible neck gaiter that can be pulled up over one's head for sun coverage ($12 at Amazon). This does not impede use of a face mask as it is very thin and flexible material, and offers excellent sun protection for ears and neck. This also minimizes the introduction of the potentially toxic compounds present in many sunscreens, to the often-sensitive small pond environments.

Leave behind the dive-fins. Pond environments are smaller than the open coast, and fins are not really necessary. They also do a lot to disturb sediments, and local benthic communities, especially around the more public access points. This will slow you down, and that is also a good thing. It encourages observation of more natural behaviors among the pond's denizens as they are less alarmed by one's approach.

Become horizontal. Walk-ins massacre soft-bodied organisms that have had no opportunity to adapt to foot traffic. This is true of both the inland ponds and the coastal intertidal community. A good rule of thumb is that every step is a killing step, and the sooner one gets horizontal in the water, the less damage one inflicts.

Limit multi-lake visits. Every pond is a natural experiment in colonization and adaptive species radiation. It could be argued that wading and diving birds bring about a constant dispersal of organisms between neighboring ponds. That said, sequential snorkels almost certainly elevate the transmission of larval organisms in the residual pond waters trapped in one's gear, and introduces an un-natural source of cross contamination. (Consider the example of our lonely *Pincatada* appearing at the outflow pipe at the Gerace Research Centre).

Be mindful and prudent when collecting. Whenever possible or practical, gently return living specimens to the location from which they were captured. Do this both to lessen the impact of your visit, and to make a statement to your students and colleagues. (This may not always be advisable if the specimen has suffered severe deterioration while in captivity.)

When studying in the Bahamas, include the Bahamians. One cannot help reflect during a year when statues of Columbus are toppling and we are forced to confront the many unearned privileges we enjoy, that we who have been so enriched by our visits to the islands have found so few ways to share our academic and research privileges with the islanders themselves (see https://www.scientificamerican.com/article/the-problem-of-colonial-science/). This isn't for lack of wanting to give back. The faculty and students I have met are eager to share in every way that they can. Good and sincere efforts have been made to partner activities at the Gerace Research Institute with the College of the Bahamas. In the spirit of broadening our support, I'd like to draw attention to a wonderful, if tiny, institute that I recently learned about on the island of Eleuthera. C.O.R.E. (Center for Ocean Research and Education), run by Dr. Owen O'Shea, is something special. These folks are "*committed to providing free marine science education to students and schools on the island of Eleuthera, to run parallel with, and complement existing government science programs. In partnership with these schools, we aim to share our vision for the sustainable use of this most valuable resource, and to educate young Bahamians with a view to cultivating the next generation of science leaders and environmental thinkers for this country.*" Dr. O'Shea is doing a lot to bring the world of marine science to the islanders themselves. We can support them at https://www.coresciences.org .

ACKNOWLEDGMENTS

Table 1.	San Salvador										
Pond name	**GPS**	**Physical characteristics**			**Habitats**						
"casual"		Tidal	Conduit identified?	Salinity (TDS g/L)	FLOC	Sand	Carbonate	Sea Grass	Calcareous algae (biotic outcrops)	Prop-roots
Reckley Hill	24-06-53 N, 74-27-37 W	YES	YES	marine	YES	no	YES	N/O	N/O	YES
Crescent	24-06-47 N, 74-27-21 W	YES	YES	marine	YES	no	YES	YES	N/O	YES
Pain	24-06-44 N, 74-27-22 W	YES	YES	marine	YES	no	YES	N/O	N/O	no
Moon Rock	24-06-39 N, 74-27-28 W	YES	YES	marine	YES	no	YES	N/O	N/O	no
Oyster	24-06-35 N, 74-27-44 W	YES	YES	marine	YES	no	YES	no	YES	YES
"Karna"	24-05-42 N, 74-26-58 W	no	no	brackish	N/O	no	N/O	no	N/O	YES
Poly Hill	24-05-05 N, 74-26-47 W	YES	YES	marine	YES	no	YES	N/O	N/O	YES
Storr's Lk.	24-03-22 N, 74-27-10 W	no	no	hypersaline	YES	no	cyanobacteria	no	N/O	YES
Big Granny	24-02-40 N, 74-29-24 W	no	no	hypersaline	YES	no	cyanobacteria	no	N/O	no
Salt	24-01-23 N, 74-27-02 W	no	no	hypersaline	YES	no	YES	no	N/O	no
South Granny	24-02-14 N, 74-29-40 W	no	no	hypersaline	YES	no	no	no	N/O	no
South Stout	23-58-11 N, 74-30-44 W	?	no	marine	YES	no	N/O	N/O	N/O	YES
"Merman"	23-57-44 N, 74-30-29 W	YES	YES	marine	YES	no	YES	N/O	N/O	YES
(Airmail) *"Mermaid"*	23-57-54 N, 74-30-53 W	YES	YES	marine	YES	no	YES	N/O	YES	YES
Clear Pond	23-58-24 N, 74-32-49 W	YES	YES	brackish	YES	no	N/O	N/O	N/O	N/O
No-name 1	23-59-52 N, 74-30-30 W	?	no	marine	YES	no	N/O	N/O	N/O	YES
No-name 2	23-58-24 N, 74-30-45 W	?	YES	marine	YES	no	YES	N/O	N/O	YES
William's Pond	24-00-47 N, 74-30-59 W	YES	YES	marine	YES	no	N/O	N/O	N/O	YES
6-Pack	24-03-25 N, 74-29-21 W	no	no	> marine	YES	no	YES	YES	N/O	no
Little Lk	24-03-01 N, 74-31-09 W	no	YES	marine	YES	no	YES	N/O	N/O	YES
Long Lk	24-03-46 N, 74-30-22 W	no	no	> marine	YES	no	N/O	N/O	N/O	N/O
Flamingo	24-03-57 N, 74-30-47 W	no	no	marine	YES	no	YES	N/O	N/O	N/O
Osprey	24-06-43 N, 74-27-52 W	YES	YES	> marine	YES	no	N/O	N/O	N/O	YES
Wild Dilly	24-06-36 N, 74-27-36 W	YES	YES	marine	YES	no	YES	no	N/O	YES

Table 2.	Eleuthera										
Pond name	**GPS**	**Physcial characteristics**			**Habitats**						
"casual"		Tidal	Conduit identified?	Salinity (TDS g/L)	FLOC	Sand	Carbonate	Sea Grass	Calcareous algae (biotic outcrop)	Prop-roots
1. (?)	25-23-56 N, 76-33-40 W	N/O	N/O	marine (?)	N/O	N/O	N/O	N/O	N/O	N/O
2. Sweetings Pond	25-21-52 N, 76-31-06 W	YES	YES	marine (?)	firm	N/O	YES	YES	red algae	YES
3. Turtle Lake	25-10-23 N, 76-12-43 W	N/O	N/O	marine (?)	YES	N/O	N/O	N/O	N/O	YES
4. Little Oyster Pond	25-09-41 N, 76-12-20 W	N/O	N/O	marine (?)	YES	N/O	N/O	YES	N/O	YES
5. Great Oyster Pond	25-09-39 N, 76-12-17 W	YES	N/O	marine (?)	YES	N/O	YES	YES	red algae	YES
6. Great Fish Pond	25-08-26 N, 76-09-19 W	N/O	N/O	marine (?)	YES	no	no	N/O	red algae	YES
7. *"Peanut" Synaptula*	25-07-35 N, 76-08-44 W	N/O	N/O	marine (?)	YES	no	no	no	YES	YES
8. Great Pond	25-08-04 N, 76-08-05 W	N/O	N/O	marine (?)	YES	no	N/O	?	no	N/O
9. Great Pond (S)	25-08-04 N, 76-08-03 W	N/O	N/O	marine (?)	YES	no	N/O	?	no	N/O
10. (?) "Big *lagoon*"	24-55-11 N, 76-08-55 W	YES	N/O	MARINE	YES	N/O	N/O	N/O	N/O	YES
11. (?) "Nurse Shark"	24-54-44 N, 76-08-37 W	YES	N/O	MARINE	YES	N/O	YES	???	N/O	YES
12. Red Pond	24-53-29 N, 76-08-28 W	no	N/O	marine (?)	YES	no	cyanobacteria	YES	no	N/O
13. (?)	24-46-30 N, 76-11-10 W	N/O	N/O	marine (?)	YES	no	YES	no	N/O	no
14. (?) "hawksbill"	24-43-46 N, 76-12-42 W	N/O	YES	marine (?)	YES	no	YES	no	no	no
15. (?)	24-43-20 N, 76-12-40 W	N/O	N/O	marine (?)	YES	no	N/O	no	N/O	YES
16. (?) "blue lagoon"	24-46-44 N, 76-17-15 W	YES	N/O	MARINE	no	YES	YES	YES	no	no

Note: N/O indicates "*not observed*". Cyanobacteria indicates carbonates presumed to be deposited by biotic processes (cyanobacterial mats or stromatolite).

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