ADAPTATIONS TO LIFE IN MARINE CAVES

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Summary

Inland (anchialine) and submarine caves in limestone and volcanic rock are extreme environments inhabited by endemic, cave-adapted (typically eye and pigment reduced) fauna. Specialized cave diving technology is an essential tool to investigate this habitat. A number of new higher taxa are represented with some closely related species inhabiting caves on opposite sides of the Earth suggesting an ancient origin. Because many of these species are found only in a single cave, pollution or destruction of caves will result in their extinction.

1. Introduction

1.3 Definition of anchialine and marine caves

Anchialine caves are partially or totally submerged coastal caves in volcanic or karstic limestone terrain that contain tidal, marine waters having a longer (months to years) residence time with this habitat. Such caves are locally called "cenotes" in the Yucatan Peninsula of Mexico and "blue holes" in the Bahamas and Belize. Frequently, they possess highly stratified water masses, with surface layers of fresh or brackish water, separated by a thermo-, chemo-cline from underlying fully marine, low dissolved waters. Animals restricted to the anchialine habitat show pronounced morphological, physiological, biochemical and behavioral adaptations and are termed stygofauna or stygobites. In areas such as Yucatan, both freshwater and marine stygofauna inhabit the same caves.

In contrast, marine caves are located either directly on the coast or wholly submerged beneath the sea floor and contain marine waters that freely exchange with the sea on each tidal cycle. The stygophilic fauna of marine caves can also be found in suitable habitats outside of caves and lack specialized adaptations for subterranean life. Moderate to strong tidal currents are present in many marine caves. As a result, encrusting, filter-feeding animals such as sponges, hydroids, anemones, tube worms and even some corals may completely cover all hard surfaces. Other organisms are swept into caves by tidal currents but which only can survive there for short periods of time are termed accidentals. Some species such as fish, lobster and mysids seek shelter within marine caves but must venture out into open waters to feed and are classified as stygoxenes.

Some extensive marine caves extend far and/or deep enough so that a more or less gradual transition in water residences times takes place and conversion occurs to a true anchialine habitat. Similarly, a number of inland anchialine systems have submerged entrances in the sea with significant water exchange occurring in these sections of the

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cave but with a transition to anchialine characteristics and fauna taking place as distance from the sea increases and impact of tidal exchanging water declines.

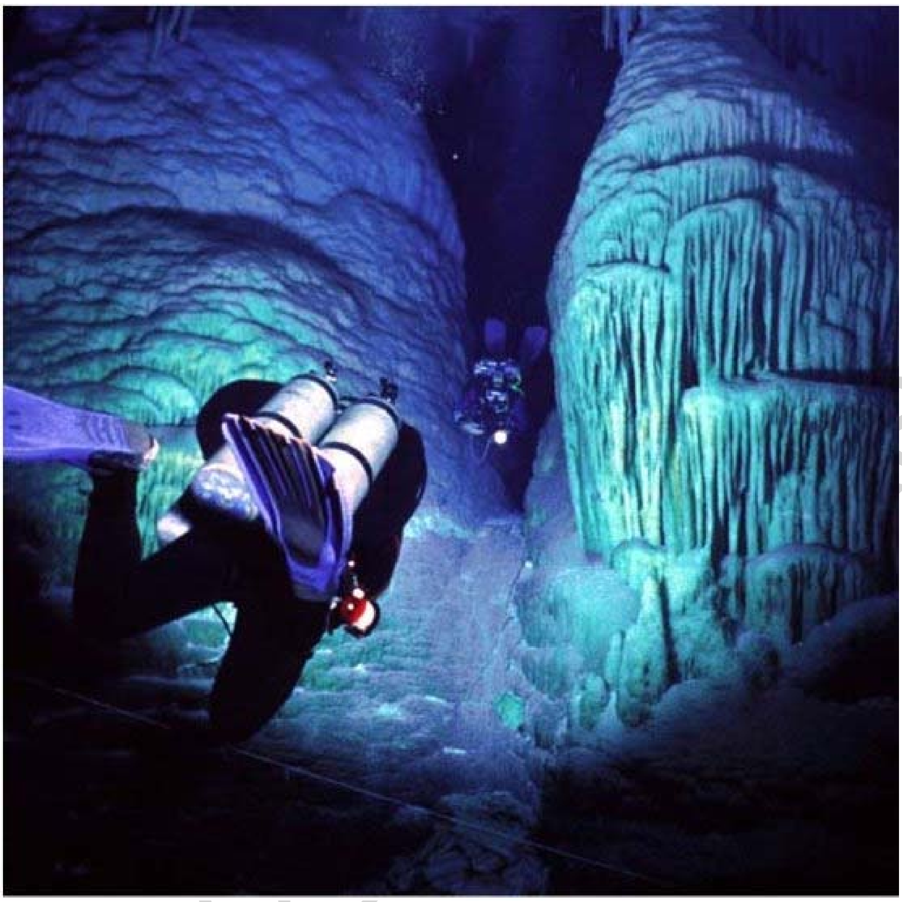

Figure 1. Cave divers swim between two enormous submerged stalagmites in Crystal Cave, Bermuda. Since such speleothems only form in air by dripping water, their presence in underwater caves is proof that the caves must have been dry and air-filled for considerable periods of time.

1.4 Biological significance

Anchialine cave contain a rich and diverse, endemic, stygobitic fauna, but, due to the technological demands and potential dangers of cave diving, are relatively unstudied. These habitats serve as refuges to "living fossil" organisms, e.g., members of the crustacean class Remipedia, and to animals closely related to deep sea species, e.g., the galatheid crab *Munidopsis polymorpha*. Such cave animals typically possess regressed features including loss of eyes and pigment. For reasons that are as yet unclear, the invertebrate fauna is dominated by crustaceans and includes the new class Remipedia, plus 3 new orders, 9 new families, more than 75 new genera and 300 new species. This extraordinary degree of novelty qualifies anchialine habitats as uniquely important. Since anchialine species commonly have a highly restricted distribution, often being found only in a single cave system on one island, pollution or destruction of caves will result in their extinction.

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Stygobitic anchialine fauna often show highly disjunct biogeographic distributions, inhabiting caves in isolated locations on opposite sides of the Atlantic and Pacific Oceans, as well as in the Mediterranean, and are considered Tethyan relicts. Various hypotheses have been proposed to explain the origin of anchialine fauna. In general, these involve either vicariance (geological) or dispersal (biological) processes. Perhaps molecular genetic comparisons of cave populations from distant locations may help provide data for determining the age and dispersal sequence of anchialine stygobites.

Figure 2. A cave diver uses a Megalodon closed circuit rebreather with full face mask to collect a small *Typhlatya* shrimp from a cave in Yucatan. Rebreathers recycle expired gas so that no bubbles are produced

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1.3 Adaptation

The interactions of freshwater, seawater, and limestone in anchialine caves create a unique set of challenges for the organisms that reside there. Stygofauna have adapted to cope with constant low oxygen conditions in an energy limited environment. Additionally, the lack of light results in little or no diurnal or seasonal fluctuation in productivity. Without light, organisms receive no visual information for orientation or communication and must function with an absence of timing mechanisms.

Adaptations to marine caves may be morphological, behavioral and physiological. As a result of both food scarcity and hypoxia, there is a high selective advantage for economy of energy observed in many phyla.

Possible adaptations as a result of this selective force are: morphological features resulting in improved food finding capability, starvation resistance, and reduction in energy demand via reduced metabolism.

2. Geological origins, age and distribution of anchialine habitats

Anchialine caves occur in both volcanic rock and karstic limestone. Lava tube caves form during volcanic eruptions of basaltic lava. They typically occur relatively close to the earth's surface and are thus relatively short lived (thousands to a few tens of thousands of years).

Anchialine lava tubes can start on land and extend out past the coastline, beneath the seafloor, or can form from submarine eruptions. Anchialine lava tube caves are known from the Canary Islands, Galapagos Islands, Hawaii and Western Samoa. The longest of these is the Jameos del Agua (Atlantida Tunnel) on Lanzarote in the Canary Islands, the submerged portion of which extends 1.6 km out from the coastline, reaching a depth of 50 m.

The most extensive of the known anchialine habitats are solutionally-developed limestone caves that typically contain both fresh and marine waters. Such caves are sometimes referred to as flank margin caves and were formed by mixing dissolution in a fresh groundwater lens.

The largest anchialine cave is Sistema Sac Actun¸ located on the Caribbean coast of the Yucatan Peninsula in Mexico and containing 153.5 km of surveyed underwater passages interconnecting at least 111 cenote entrances. Extensive anchialine limestone caves are also known from the Bahamas, Bermuda, Belize, Dominican Republic, and Bonaire in the Caribbean, plus the Balearic Islands and Sardinia in the Mediterranean. Smaller anchialine caves are present on many islands in the Indo Pacific and in Western Australia.

Limestone caves last much longer than lava tubes and can be hundreds of thousands to many millions of years old. Commonly, sizable underwater stalactites and stalagmites occur to depths in excess of 50 m in coastal limestone caves (Figure 1). Such speleothems can only form in air indicating that these caves must have been dry and air-filled for long periods of time when glacial sea levels were as much as 130 m lower than today. The last low stand of Ice Age sea level occurred only 18,000 years ago.

Coastal tectonic faults that extend below sea level constitute another form of anchialine habitat. On Santa Cruz in the Galapagos Islands, vertical faults in coastal volcanic rock are locally called "grietas".

Wedged breakdown blocks have partially roofed over submerged portions of grietas so that are in total darkness. Similar faults are present in Iceland. Fault caves also occur in uplifted reef limestone on the island of Niue in the Central Pacific, produce deep chasms containing anchialine pools.

The Ras Muhammad Crack in the Sinai Peninsula consists of a water-filled crack in an elevated fossil reef formed by a 1968 earthquake. Many of the ocean blue holes of the Bahamas consist of submarine faults running parallel to the platform edge. Ocean blue holes typically exhibit exceptionally strong, reversing tidal currents created by an imbalance between tides on opposite sides of the islands.

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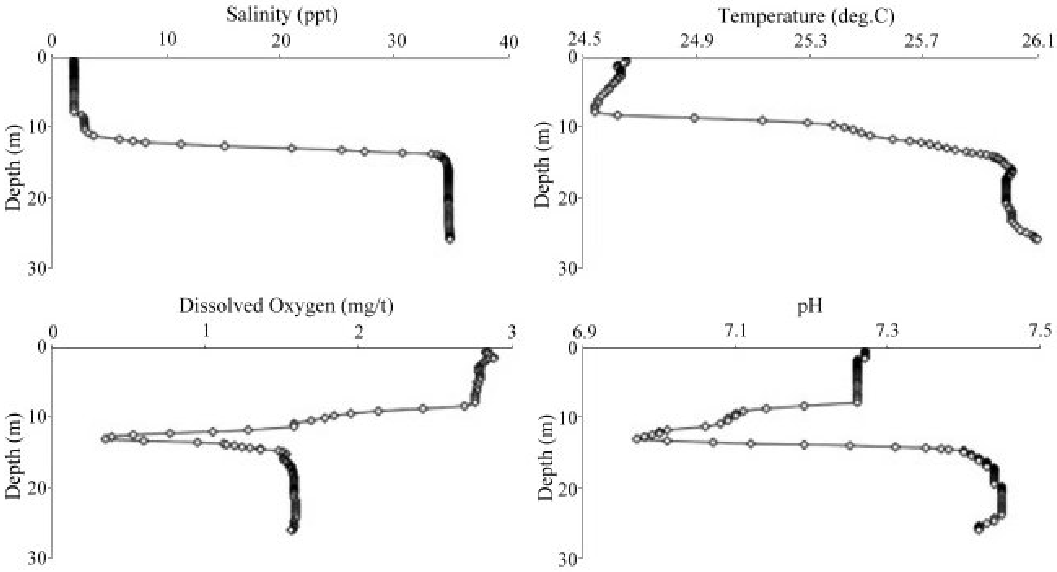

Figure 3. Depth profiles of salinity, temperature, dissolved oxygen and pH from an anchialine cave, Cenote 27 Steps, in Akumal, Mexico taken on 7 December 2003 using a YSI 600 XLM multi-parameter water quality monitor. Individual measurements, indicated by ◊ symbol, were taken at 4 second intervals between the surface and 26 m water depth.

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3. Anchialine cave ecology

3.1 Diving investigations

Since anchialine stygobites are commonly found only at significant depths and/or distances from cave entrances, cave diving is an essential component to collection and study of anchialine fauna. Cave diving requires specialized training, equipment and techniques, since a direct assent to the surface is not possible and divers may be hundreds of meters from access to the surface.

In case of equipment failure or loss of air supply, cave divers must have readily available backups. Special techniques for cave diving may include the use of side-mounted instead of back-mounted scuba tanks to allow divers to pass through low bedding plane passages.

Closed circuit rebreathers (Figure 2), which recycle the diver’s exhaled gases, reduce the amount of percolation, i.e., silt dislodged from cave ceiling or walls by exhaust bubbles produced in conventional, and also lessen contamination of the low dissolved oxygen cave waters.

Deeper dives, below 40 m depths, require use of special breathing gas mixtures that replace nitrogen with helium to reduce the effect of nitrogen narcosis. Since many cave dives are for longer durations and/or to deeper depths, they frequently involve long decompression.

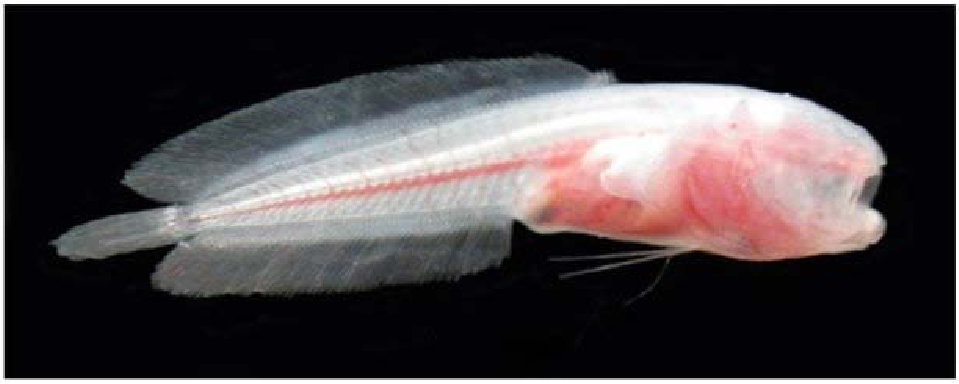

Figure 4. The Yucatan cave fish *Typhliasina pearsei* belongs to the Family Bythitidae. It is widely distributed in freshwater cenotes throughout the Yucatan Peninsula

3.2 Physical and chemical characteristics

A high degree of vertical stratification occurs in most anchialine caves (Figure 3). The largest changes in chemical and physical parameters typically occur at the halocline where fresh or brackish water is separated from underlying fully marine waters.

On islands and in some continental regions such as Yucatan and Western Australia, freshwater occurs as in the shape of a lens with thickness increase in a direct relationship with distance inland from the coast. In Yucatan for example, the depth of the halocline and corresponding thickness of the freshwater lens, increases from 10 m at 2 km distance inland to 20 m at 10 km.

Water temperature generally increases with depth, while dissolved oxygen decreases. Warmer waters below the halocline could be due to geothermal heating at depth and/or evaporative cooling at the surface. In the lightless interior of caves, there are no plants and hence no photosynthetic oxygen production, while stable and stratified water masses restrict vertical mixing and exchange of oxygen with surface waters.

Where deep, water-filled vertical shafts extend to the surface, such as in many cenotes and blue holes, the input of organic matter has resulted in total depletion of dissolved oxygen and resulting anoxic hydrogen sulfide production.

A several meter thick, cloud-like layer of hydrogen sulfide occurs just below the halocline and may reduce underwater visibility to near zero, but water clarity improves considerably below the H_2S layer. In some caves, dissolve oxygen levels can recover to 1 mg/l or less and populations of stygobitic fauna occur.

A pH minimum generally occurs at the halocline, possibly arising from microbial oxidation of organic matter suspended at the density interface and resulting CO_2 production. Increased acidity at the halocline may explain the dissolution of limestone and resulting development of cave passages at this depth.

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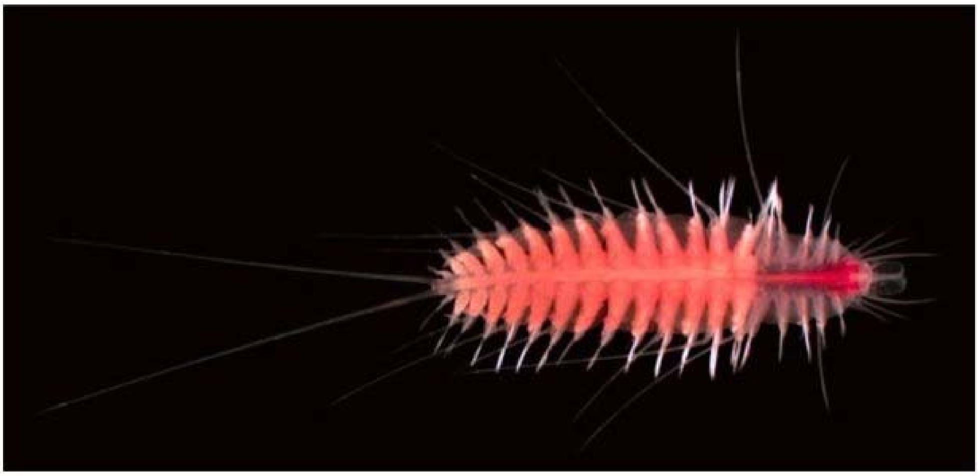

Figure 5. The polynoid polychaete worm *Pelagomacellicephala iliffei* inhabits anchialine caves in the Bahamas and Caicos Islands. This fragile animal is typically observed swimming slowly through the water column.

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Biographical Sketches

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