Palaeontologia Electronica
palaeo-electronica.org

Practice and prospects in underwater palaeontology

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ABSTRACT

Underwater deposits, especially those in phreatic caves, often contain exquisitely preserved fossils, and many represent Quaternary Konservat-Lagerstätten. Nevertheless, they are unrecognised as such by most practicing palaeontologists. This review highlights the unique contributions to palaeontology made by underwater deposits as well as the technical and practical challenges facing underwater palaeontologists. Recovery of fossils from such deposits requires specialist training, equipment, and procedures unique to these environments. Taphonomic studies of underwater assemblages are rare and hampered by difficulties in fossil recovery. Neotaphonomic experiments and observations of modern accumulations in underwater settings should be a priority for future research. Regions where such techniques might provide important new insights into Quaternary faunas and environments, not accessible through traditional palaeontological approaches, include low-lying flooded continental shelves and soil-poor karstic landscapes. Underwater palaeontology represents a largely unexplored yet significant source of fossils, further study of which will expand and enrich traditional approaches in the study of ancient organisms.

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Keywords: diving; cave; sinkhole; taphonomy; vertebrate palaeontology; Lagerstätten

Submission: 14 December 2017 Acceptance:

INTRODUCTION

The discoveries of spectacularly well-preserved fossils from underwater settings across different continents hint at a vastly underexplored environment for evidence of ancient biodiversities and organisms. To date, fossils have been recovered from the phreatic zone (drowned or flooded) of caves and sinkholes, lakes, and continental shelves and margins that have undergone marine transgression. They have been reported from

Louys, Julien. 2018. Practice and prospects in underwater palaeontology. *Palaeontologia Electronica* 21.2.22A 1-14. https://doi.org/10.26879/840
palaeo-electronica.org/content/2018/2239-underwater-palaeontology

across the globe, including Australia, Indonesia, the United States, Canada, the Bahamas, Mexico, the Antilles, Brazil, Chile, the North Sea, and Madagascar.

The first to explicitly address underwater study as important for palaeontology was the French philosopher Benoît de Maillet, who in 1797 described diving gear and techniques for underwater observation of animals and sediments, relating these to fossils (de Maillet, 1797, cited in Brooks, 1965). The invention of self-contained breathing apparatus (scuba) greatly assisted all forms of underwater exploration. Other techniques employed in the early years of underwater palaeontology, including using oceanographic equipment, cofferdams, air cambers, and glass bottom buckets (Brooks, 1965) have largely if not entirely been abandoned since the introduction of and technical and safety improvements to scuba systems. These improvements permit the exploration of underwater environments previously deemed too dangerous or too difficult to access, as well as a more systematic approach to fossil recoveries. The other major means of recovery underwater fossils, dredging, continues to produce tonnes of fossils per year (Post, cited in Bailey and Flemming, 2008), although necessarily these are collected with extremely limited contextual information.

Many underwater sites have produced examples of "the most complete" or "the largest collection" of various extant and extinct mammals, particularly those reported from underwater caves. While all caves are renowned for their preservation of complete or large collections (e.g., Harris, 2005; Jass and George, 2010; Price et al., 2017), fossils situated in continuously or near-continuous underwater environments are much less subject to post-depositional disturbance by biotic and abiotic agents that can disturb or destroy elements (for example, porcupines and flood events, respectively; Louys et al., 2017). Thus, the underwater environment can provide an additional level of preservation, complementing other environmental factors commonly found in above-water cave deposits, which increase the likelihood that fossils will be articulated and well preserved.

The rivers and natural springs of Florida have produced several complete or near-complete mammoth and mastodon skeletons (Webb, 1976), as well as hundreds of isolated specimens of terrestrial and aquatic vertebrates (Webb and Simons, 2006). Many have been recovered from natural springs and rivers in Florida since at least the 1930s, originally by glass bottom buckets and picking fossils from river beds, and later by professional divers undertaking excavations on behalf of archaeologists (Simpson, 1930 in Brooks, 1965; Dunbar et al., 1989; Webb, 2006). Early reports of underwater cave fossils recovered with scuba gear in 1968 concerned the discovery of various marsupial fossils from Green Waterhole Cave (also known as Fossil Cave; Figure 1) in the Mt Gambier region of South Australia ("South-East has Tourist Attraction Underground" The Border Watch, 27 February 1968, cited in Pledge, 1980). This site, as well as numerous others in the Mt Gambier area, eventually produced hundreds of incredibly well-preserved fossils of extinct and extant marsupial remains (Pledge, 1980; Reed and Bourne, 2000)

FIGURE 1. Green Waterhole Cave in Mt Gambier, South Australia. This site has produced many exquisitely preserved Pleistocene fossils, mostly of large kangaroos. 1. Overview of the site, arrow indicates the cave entrance from which most fossils were extracted. 2. View from arrow into cave entrance, showing current water level and beginning of talus cone.

including some of the first complete skulls of the extinct kangaroo *Simosthenurus*.

Other sites around the world have been equally productive. Aven Cave in Madagascar produced the largest assemblage of fossil lemurs ever discovered (Rosenberger et al., 2015). La Jeringa in Parque del Este, Hispaniola, produced the first and most complete specimen of the primate *Antillothrix bernensis* (Rosenberger et al., 2011) in addition to numerous sloth and rodent remains (Cooke, 2011). Oleg's Bat House Cave in Hispaniola produced a diverse bat assemblage as well as several almost complete crocodile skeletons of a new species to the island (Cooke, 2011). Underwater dredging of the North Sea has produced thousands of fossils, extinct proboscideans being particularly noteworthy (Mol et al., 1999). Stiva Cave, a marine cave system situated off the coast of Bali, has preserved several large-bodied mammals from the surface of the cave sediments including deer and elephants (Harbowo et al., 2017). Medium- and large-bodied species, including fossil tayassuids (peccaries) were recovered from Caverna do Japonês and Nascente do Formoso in Brazil (Dutra et al., 2017; Salles et al., 2006). On the Yucatan Peninsula, Mexico, in addition to several underwater human burial sites, four flooded palaeontological sites have been recorded preserving horses, camelids, giant armadillos, tapirs, and proboscideans (González González et al., 2008).

Unusual for underwater sites, Sawmill Sink in the Bahamas produced not only exceptionally well-preserved mammal remains but also macro- and micro-plant fossils from a peat sequence (Steadman et al., 2007). Equally, Page-Ladson Site in Florida preserved rich accumulations of mastodon dung, including coherent boluses of digesta (Newsom and Mihlbachler, 2006), and corticosteroids recovered from these deposits have been attributed to *Mammut* (Webb and Simons, 2006).

The extreme nature of underwater environments, particularly in underwater caves, holds great potential for the preservation of the hard parts of entire animals in an undisturbed a context. At the same time, the very inaccessibility of these environments presents unique and potentially life-threatening hurdles for their accurate documentation and successful recovery. In this paper, I summarise previous underwater palaeontology excavations and recovery efforts, and discuss the advantages, technical considerations, and physical challenges of working in such environments. On the basis of these, suggestions for future best practice approaches for underwater palaeontology are presented. The focus here is on non-anthropogenic accumulations of vertebrate remains. A well-developed body of literature exists for the study of submerged archaeological sites, including some addressing zooarchaeological remains (e.g., Bell and Elkerton, 2008, Greenfield et al., 2006, Dunbar, 2006). Likewise, the forensic analysis of underwater environments is a growing field of research (e.g., Becker, 2013). Although some overlap exists between forensics and palaeontology, the decay of bodies underwater is not specifically discussed here, nor are taphonomic investigations of shipwrecked sites. This review is primarily concerned with the deposition, preservation, and recovery of vertebrate remains in underwater settings, which to date appear confined to Quaternary deposits. Fossils native to underwater systems, such as the corals making up the limestone of karst regions hosting caves or the lithified shell beds of marine systems, are not discussed.

GEOLOGICAL CONTEXTS

Underwater fossil deposits largely occur in two main contexts: the phreatic zone of caves (inclusive of sinkholes, caverns, cenotes, and blue holes) and low-lying continental shelves. Underwater sites from the Yucatán Peninsula, Mexico, Madagascar, Brazil, Bahamas, Florida, and Australia are all examples of the former. The extent of phreatic zones in caves and sinkholes are controlled by groundwater levels, in turn a function of stream flows and channel geometries at the local scale, and regionally precipitation and sea level (particularly for sites close to the coast) at regional scales (Smart and Worthington, 2004; Mylroie, 2004; Webb, 2006). Continental shelf deposits, for example the underwater caves in Bali and the offshore localities of Central Chile and the North Sea, are underwater as a result of flooding of low-lying sections of the shelf and thus resultant from sea-level rises. While deposits in caves, and to a lesser extent sinkholes, can occur in both phreatic and vadose environments, those on the continental shelf will almost always occur in a terrestrial or semi-terrestrial environment first. In a similar scenario, fossils recovered from lake settings may be the result of changes in lake levels resulting in flooding near-shore, terrestrial depositional environments (Jass et al., 2018). Thus, continental shelf deposits, and to a lesser extent lacustrine deposits, are dictated primarily by their geographical location rather than their geological context, the latter of which can encompass any sedimentary environment likely to preserve fossils. The recovery of marine vertebrates in shallow offshore settings (Noakes et al., 2009) and those deposited in lakes by falling through ice (Jass et al., 2018) are probably rare exceptions to the major underwater deposit types.

CHALLENGES AND TECHNICAL DIVING CONSIDERATIONS

The biggest challenges facing researchers in underwater palaeontology relate to physical factors such as the depth of the deposits underwater, flows or currents, and in the case of caves (and to a lesser extent sinkholes and caverns), the presence of an overhead environment, constricted and/or lengthy passages, and 'silting up' of underwater environments. Exploration and study of submerged caves is considered one of the most highly specialised and potentially dangerous forms of diving (Iliffe and Bowen, 2001). Other hazards particular to cave diving include psychological pressures and task loading (Iliffe and Bowen, 2001), as well as limited dive time concerns related to both decompression from working at depth and safe return from diving in overhead environments.

Fossil deposits can be found in deep waters through lengthy passages. In Japonês Cave, for example, fossil material was found at a maximum depth of 43 m at a distance of 220 m from the entrance (Salles et al., 2006). Although Aven Cave is a sinkhole, it also preserves deep horizontal passages that required cave diving skills to access (Rosenberger et al., 2015). Depth concerns can be somewhat mitigated by diving with gases other than air. In Georgia for example, divers excavating off-shore used 36% NITROX gas mixtures to allow for greater safety underwater as well as shorter surface intervals (Noakes et al., 2009; however, these authors did not report on the depth the specimen was recovered from). Deeper and/or longer dives require specialist training and different gas mixtures beyond the prerequisites of standard cave diving training.

Because of the ease of access to diving equipment and open water dive sites, divers can be lulled into believing that scientific cave diving is merely a straightforward extension of normal scientific diving experiences (Brooks, 1965). On the contrary, scientists diving in caves must first be highly competent and experienced cave divers before embarking on any scientific cave diving (Iliffe and Bowen, 2001). This requires a considerable investment in time and resources for training, practice, and equipment. Cave diving organisations often regulate or administer cave diving training and accreditation in certain countries. For example, in Australian caves the Cave Diving Association of Australia (cavedivers.com.au) administers dive training and control access to many caves.

Local laws affecting the collection of fossil remains will often equally apply to underwater settings, however, the unique environments represented by underwater palaeontological sites might not be adequately defined in existing legislation. For example, Noakes et al. (2009) described some of the difficulties they encountered in obtaining permits for the excavation of underwater remains of some antiquity that did not fit conformably within the jurisdiction of existing local and national agencies.

RECOVERY TECHNIQUES

Most often, specimens are picked up from the sedimentary interface where they are commonly first observed (Figure 2.1) or just below, e.g., within arm reach (Newton, 1988), by divers directed by palaeontologists on the surface. Specimens collected in this way can be marked with identification tags, then mapped in relation to reference lines established previously (e.g., Newton 1988; Steadman et al., 2007). However, significant time between tagging and mapping may result in overconscientious recreational divers removing tags in an effort to 'clean' the site, as occurred in Green Waterhole Cave (Pledge, 1980).

Radial reference lines around irregular surfaces such as talus cones have been used in both the Bahamas and South Australia, with fossils plotted relative to distances from marker poles and depths (Newton, 1988; Steadman et al., 2007). The use of a safety line as a survey instrument, as enacted in early excavations in Mt Gambier, proved unreliable (Pledge, 1980). In Page-Ladson Site, Florida, recovery of fossils and artefacts were successfully extracted in pre-defined excavation units of variable dimensions, allowing for systematic documentation of stratigraphic and locality information for each specimen brought to the surface (Latvis and Quitmyer, 2006). This was accomplished using PVC pipe frames or aluminium-angle frames fixed to metallic tubing driven into the river sediment, with bubble levels and meter scales used to record horizontal and vertical distances of specimens relative to marks on the frame. River bottom coordinates were related to terrestrial coordinates by establishing a river gauge datum, and correlating coordinates of both systems to the datum (Latvis and Quitmyer, 2006).

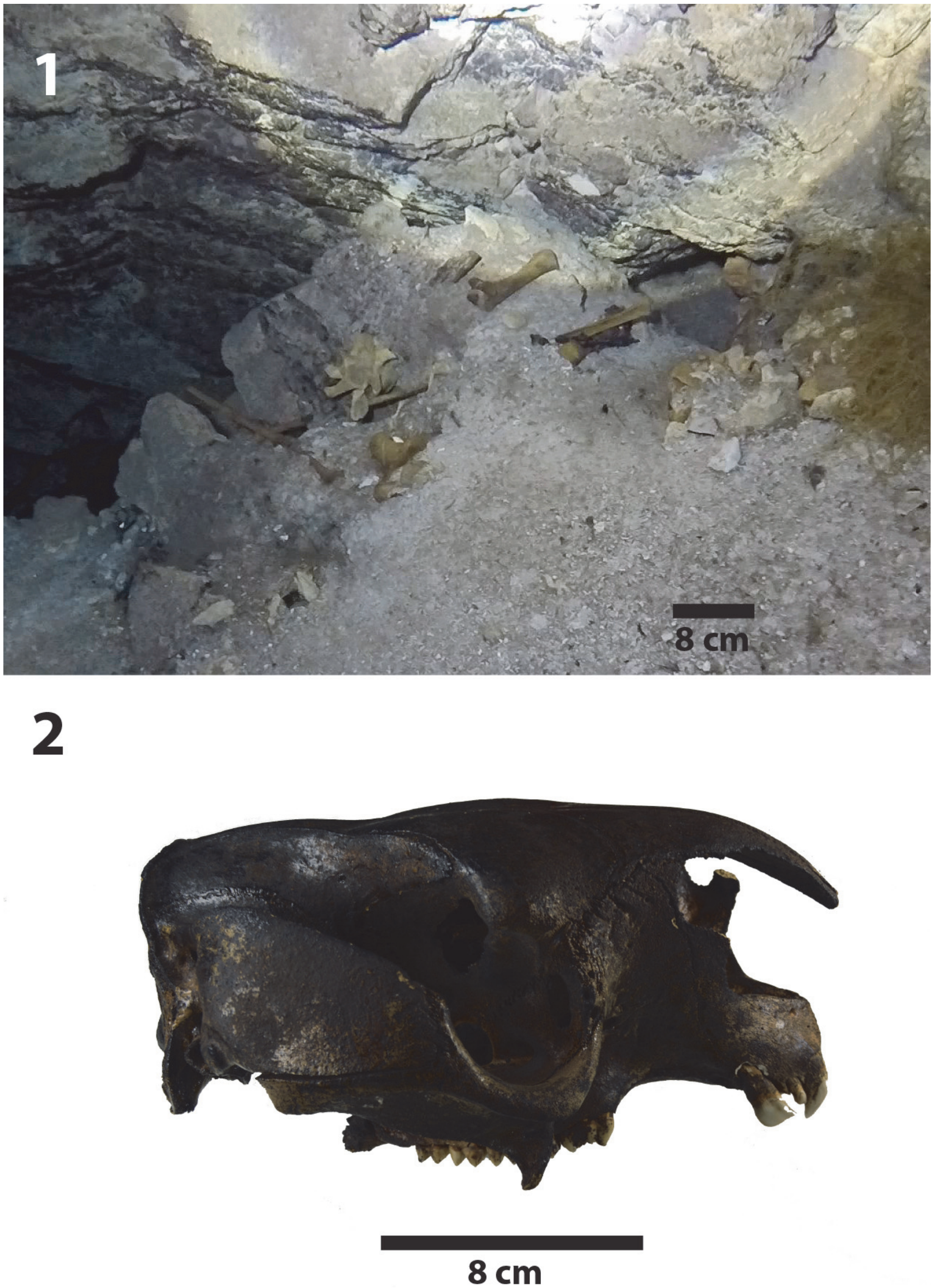

FIGURE 2. Examples of fossils from underwater caves. 1. Fossils lying on the sedimentary floor in Kilsby's Sinkhole, Mt Gambier, South Australia. 2. Skull of *Simosthenurus maddocki* from Green Waterhole Cave, showing the characteristic black staining of the majority of fossils from this deposit.

Visibility can be a severe limiting factor in underwater work (Figure 3). Even minimal excavation can pose problems in underwater caves, as any disturbance of the cave floor can result in the 'silting up' of the cave passage, limiting visibility to a few centimetres or less. In order to minimise silting of the site, González González et al. (2008) executed fossil extractions only at the end of each dive. Nevertheless, it takes significant time for silt to resettle, limiting repeat diving by different teams at the same site. Visibility can also be impacted by diver disturbance of bacterial mats on the cave roof. In the Bahamas, divers used closed-circuit mixed-gas rebreathers in an effort to minimise disturbance to such mats, thereby increasing visibility while work progressed underwater (Steadman et al., 2007). Divers in the Florida rivers encountered a very different visibility issue. There, sediment load suspended in the water was minimal; however, the high tannin concentrations of the water from the decay of vegetation in the swamps restricted visibility to less than 3 m below the surface (Latvis and Quitmyer, 2006). This issue was overcome with the use of high wattage underwater lights which helped penetrate the tannic-stained waters (Figure 3).

Although Brooks (1965) predicted that the airlift would not find wide use in palaeontology, Salles et al. (2001) describe airlift equipment they used in the excavation of Buraco do Japonês cave. An airlift produces a pressure differential in order to shift water and suspended sediment from the area of interest to the end of the airlift system. Such equipment is often used in commercial dredging and underwater archaeology, although is limited to deeper sites. Salles et al. (2001) reported shifting 8640 litres of water and suspended sediment using an airlift over the course of 47 hours of diving (9 hours of airlift time). The outflow was sieved on the surface, from which the team recovered 550 fossil specimens. In shallower waters, a water dredge is usually more effective. Carabias et al. (2014) reported using a 3 inch induction water dredge for excavation, although the efficacy of this equipment was not discussed in any detail. Latvis and Quitmyer (2006), however, provide a detailed and thorough description of how dredges were used to great effect to excavate Page-Ladson site. There, 1 x 1 x 0.2 m squares were excavated by divers working the dredge in teams of two, with all material sieved, sorted, and dried on the surface.

In some cases, fossils are lithified in situ and have to be mechanically extracted. Noakes et al. (2009) describe the removal of a whale mandible from a cemented shell bed off the coast of Georgia, USA. They used hand tools including a slide hammer, hand pick, and hammer and chisel to remove the overlying sediment. This process took 124 dives by nine divers to extract the 1.5 m, 22 kg mandible. Brooks (1965) also advocated similar mechanical excavation techniques for underwater deposits in Florida.

In deep sites, such as those found in Mexico, decompression considerations meant that divers were only able to spend a few minutes per dive at the sites (González González et al., 2008). Time is one of the biggest differences between excavations conducted in dry or terrestrial settings and those undertaken in underwater settings. Divers are limited not only in terms of the amount of time they can spend underwater on each individual dive (dictated by depth, previous dives, and gas mixtures and volumes used), but also the time of day they can dive (particularly for marine environments). Furthermore, underwater scientists have to weigh the risks of leaving a partially excavated specimen in situ between dives, cognisant that at any moment further dives might not be possible and that specimens might be subsequently destroyed by storms, strong currents, or unscrupulous visitors. Due to extreme time pressures, underwater excavations cannot be expected to be completed at the same level of precision and attention to detail afforded to terrestrial counterparts. While time pressures are not unique to underwater palaeontologists, they have the potential of being significantly more acute than experienced in more traditional excavations.

FIGURE 3. Diver excavating in low visibility conditions of the Aucilla River, Florida, under the cone of a 1000-W underwater work light. Photo credit: Tim Barber. Reproduced from Latvis and Quitmyer (2006; figure 1.9) with permission from Springer Nature.

In order to maximise their time in each dive, González González et al. (2008) first established baselines in the cave and undertook 3D mapping relative to these baselines. Documentation was undertaken with digital cameras, video, and 35-mm photography. These were analysed directly after each dive on the surface. Likewise, photography and video formed an integral part of excavations at Page-Ladson Site (Latvis and Quitmyer, 2006). Schubert et al. (2017), López et al. (2016), and Rosenberger et al. (2015) also used 3D photogrammetry to record the in situ context of select specimens, greatly aiding site and depositional interpretations.

Successful recovery of bones continues well beyond their extraction from an underwater site. Because the bonds between the organic (primarily collagen) and inorganic (hydroxyapatite) constituents of bone matrix are degraded by water (Stone et al., 1990), specimens recovered from such systems must be specially treated to avoid physical deterioration of mineralised specimens after extraction from their flooded milieus. Drying wet bone can produce a range of damage including shrinking, twisting, cracking, and delamination, such that conservation of specimens may require controlled drying procedures and consolidation (Stone et al., 1990; Rogers, 2004; Grant, 2007). Different researchers have used different techniques depending on site-specific characteristics. González González et al. (2008) employed water-filled boxes for fossil extraction, ensuring the same geochemical composition of the water on recovery. Cartajena et al. (2013) reported using successive water baths to remove soluble salts from specimens, a process necessary for any saltwater deposits (Rogers, 2004). Remains from Oleg's Bat House Cave in Hispaniola and fossils from Mt Gambier in South Australia were first washed, slowly dried, and ultimately preserved using chemical hardeners (Pledge, 1980; Cooke, 2011). Stone et al. (1990) recommended the use of an acrylic emulsion in their conservation of material from a wetland site in Florida, which allows for the treatment of bone while still wet. Any air-drying of waterlogged bone should be slow, with temperature, humidity controlled and monitored whenever possible, but particularly when the bone is soft (Grant, 2007). As each site is different, experimentation with test samples of bones is highly recommended (Grant, 2007).

Each site has unique environmental conditions that will affect bones differently, with high pH water producing faster degradation of bone organics and datable collagen. The size of bones, the temperature of the water, and the tanning effect of some organics, on the other hand, can act to preserve collagen (Pfretzschner, 2004). Nevertheless, circumstances favouring the preservation of collagen appear not to be the norm for underwater deposits, at least based on reported dating efforts these sites. For example, radiocarbon dating of fossil peccaries from Caverna do Japonês and Nascente do Formoso (Dutra et al., 2017), presumed to be Late Pleistocene or Holocene in age on the basis of associated faunas, produced no reliable ages (although the details of the dating attempts were not provided, and Dutra et al. (2017) further noted that their fossil remains displayed different levels of mineralisation, implying some measure of time-averaging of the deposit). Likewise, bones from a drowned continental shelf setting did not preserve sufficient collagen for radiocarbon dating despite most likely being only ca. 16 ka (Cartajena et al., 2013). While bones from the peat layers in an inland blue hole in the Bahamas produced reliable radiocarbon ages, several bones from a nearby flooded owl roost did not (Steadman et al., 2007). Attempts at radiocarbon dating of fossil from Mt Gambier proved ineffective (Newton, 1988). Conversely, a whale mandible from an offshore marine setting was successfully radiocarbon dated by analysing the bioapatite portion of the bones (Garrison et al., 2012). Determining the specific factors responsible for the preservation of datable bone in flooded settings will likely prove useful for future research in underwater palaeontology.

TAPHONOMIC ANALYSIS

Previous Taphonomic Studies of Underwater Deposits

Very little research into taphonomic processes operating in underwater palaeontology sites exists (Cartajena et al., 2013). One of the few studies specifically examining taphonomy of an underwater site examined fossils recovered from a flooded marine shelf (Cartajena et al., 2013; López et al., 2016). These analyses showed slight abrasion on almost all specimens, most likely from marine action such as waves or tidal movements. They also noted surface weathering and root marks on the majority of the bones, as well as carnivore damage on a few specimens, suggesting the bones were exposed on the surface prior to immersion in water. López et al. (2016) also examined Voorhies groupings (bone dispersal categories based on element, size, shap, and density) on these fossils and the orientation angles recorded in situ in an effort to reconstruct the depositional environment, which they suggested represents a low energy flow.

In the only other major study on underwater taphonomic processes, Newton (1988) assessed several taphonomic indices in an effort to understand the formation processes of the bone deposits in Green Waterhole Cave, South Australia (Figure 1). Based on skeletal association data, Newton (1988) suggested the layout of bone deposit in Green Waterhole Cave was a function of distance travelled down the talus cone as well as topographic complexity of the travel path down the highly uneven slope of the talus. This presumed that many of the skeletons found in that site were washed into a relatively dry site, a supposition partly supported by rodent damage on several of the bones. However, she also found that the majority of the skeletons were in anatomical association, strongly suggesting in situ deposition of remains in an underwater setting. Two different modes of deposition most likely account for this discrepancy (Newton, 1988), as the rodent gnaw damage was largely restricted to the upper levels of the deposit while the well associated skeletons, presumably from floating carcasses (see below), were found towards the bottom levels of the site towards the rear of the cave. Newton (1988) found that the most abundant fauna recovered from this cave were large kangaroos, and furthermore, that these were mostly from breeding-age individuals. It was suggested that the cave acted as a natural pitfall trap (Newton, 1988); however, this does not entirely explain such a strong taxonomic and age bias, and it is likely that like dry cave deposits, taphonomic history of this underwater cave is complex, and other factors were involved in this accumulation.

In Aven Cave, small-bodied mammals were found in dense concentrations, suggesting accumulation from owl roosts or, as suggested by Rosenberger et al. (2015), some form of ‘natural sorting’. Larger specimens in this cave were found in close anatomical association, suggesting little to no post-mortem movement. Similarly, Pledge (1980), Webb (1976), and González González et al. (2008) reported that many bones in the sinkholes they examined were found in close to correct anatomical position upon first discovery, with subsequent movement and loss of elements largely attributed to unscrupulous or curious divers. Conversely, Salles et al. (2001) reported extensive signs of rolling for the specimens they recovered from Buraco do Japonês cave, suggesting significant movement of these specimens after initial deposition.

Distinguishing between dry deposits that have secondarily become flooded and deposition in already flooded environments requires the identification of taphonomic variables and signatures unique to underwater contexts. Due to the dearth of taphonomic studies dealing specifically with continuously flooded settings, distinguishing these two types of depositional environments is difficult, particularly as they represent extremes in a continuum rather than discrete states. Neotaphonomic studies as well as more in-depth analyses of flooded assemblages are urgently required to address the deficit of data regarding underwater taphonomy. Nevertheless, there are a few potential taphonomic indicators of submerged environments that have been noted in previous studies.

Taphonomy Unique to Submerged Environments

As outlined above, manus elements were rare in the Green Waterhole Cave collection (Newton, 1988), suggesting bloating and deposition in a flooded setting of at least some of the individuals recovered. Some Mexican cenotes have also preserved widely dispersed crania and autopodia, equally attributed to floating and subsequent decay of bodies after the flooding of the sinkholes (González González et al., 2008). A skeletal bias featuring articulated or semi-articulated remains without autopodia could thus be indicative of deposition in a flooded cave setting.

Underwater environments can also produce unique bone surface damage that might be diagnostic for these environments. For example, Stinnesbeck et al. (2017) reported on fragmentation and potential dissolution of parts of the cranial vault of *Xibalbaonyx oviceps* in response to exposure to cave water. González González et al. (2008) also reported on the poor preservation of their fossil remains, attributing this to salt water corrosion. Bones from the Yucatan cenotes were reported as “very light, fragmented in situ, and superficially dissolved” with the loss of almost all organics (González González et al., 2008, p. 13). Likewise, fossils from Mt Gambier in South Australia were described as “exceedingly delicate and soft” when first found (Pledge, 1980, p. 132).

The physical and chemical damage to bones produced by water, particularly in weakening the bonds between the organic and inorganic constituents, also promotes degeneration of organics in the presence of oxygen by allowing penetration of microorganisms, which attack collagen (Stone et al., 1990; Pfretzschner, 2004). Microbial action gives way to abiotic degradation after about six months, with collagen gelatinised and split into smaller and smaller protein chains, which, upon hydration, swell and produce cracks at the circumference of secondary osteons (Pfretzschner, 2004). Thus, not only does deposition of organic remains in flooded settings negatively impact collagen preservation, hindering radiocarbon dating attempts, but it also leaves characteristic damage on bone, which is discernible at the microscopic level (Pfretzschner, 2004). Such damage should not be present in bones that have lost their organic component prior to flooding. Thus, where this damage is absent, it will indicate that bones have lain on the surface for some time before flooding occurred.

In cave settings, mineral deposits can occur on the surface of bones either because of changing chemistry of the groundwater (i.e., carbon dioxide loss, oxidation, evaporation) or through the actions of microorganisms (Hill, 1982). The Mt Gambier fossils in particular are remarkable in often being covered in heavy manganese staining (Figure 2.2). In flooded deposits, precipitation of manganese is associated with etching of the surface of the fossil bone during late diagenesis, as well as occurring on the bone surface. Manganese deposits can also be found in Haversian canals and tectonic cracks and cavities inside the bone (Pfretzschner, 2004). Such indicators are discernible in histological sections, although how much these would differ from buried bones exposed to mineralised groundwater has not been tested. Nevertheless, the use of manganese staining to reconstruct taphonomic history (e.g., López-Gónzalez et al., 2006) could be a promising avenue of future research for underwater deposits.

ADVANTAGES AND FUTURE RECOMMENDATIONS

Despite the difficulties in the identification, recording, and extraction of fossils from underwater settings, such environments also provide unparalleled benefits for palaeontologists. Here, these advantages are summarised, and recommendations for future practice of underwater palaeontology by the scientific community proposed.

Fossils recovered from underwater caves are often incredibly well preserved and abundant (e.g., Rosenberger et al., 2015; Salles et al., 2001). This is because unlike dry caves, when bones are deposited in continuous or near-continuous flooded settings they are much less likely to be subject to post-depositional destruction by physical or biotic agents (e.g., weathering, mass movement events, trampling, durophagy). Due to difficulty of access, human impacts in underwater settings are also often rare to non-existent (e.g., Salles et al., 2001), such that original bone positions and associations are often preserved. In very popular cave diving locations, such as the Yucatan and South Australia, it thus becomes important that cave-diving operators and practitioners are made aware of the conservation and scientific importance of 'underwater graveyards', such that disturbance of bones is made only after consultation or collaboration with scientific professionals.

Recommendation 1. Involve and inform diving organisations associated with the flooded setting of the significance of the site and the work that may be undertaken. This can be done through consultative meetings, public presentations, and notices or articles in organisation newsletters and magazines.

Rosenberger et al. (2015) suggested that a further advantage of underwater caves lies in the presence of sedimentation, from the decay of limestone or the influx allochthonous sediment into the sinkhole, such that it might be possible to achieve a level of stratigraphic control when extracting fossils that isn't found in local dry caves. Certainly, the deposition of vertebrate fossils in sediment rich in plant macro- and microfossils in the Bahamas provided unique insights into Quaternary palaeoenvironments of the archipelago (Steadman et al., 2007). The careful systematic excavation of fossils from Page-Ladson site not only revealed two major periods of faunal accumulation directly associated with marine isotope stages 3 and 2 (Webb, 2006), but also the identification of distinct mammoth dung deposits (Webb and Simons, 2006). The use of sedimentological analyses along passages, talus cones, or submerged shelf settings (e.g., Newton, 1988; Steadman et al., 2007; Harbowo et al., 2017, López et al., 2016) can also provide useful information for the reconstruction of the post-flooding history and environments of originally dry sites. For example, Newton (1988) discerned two modes of deposition for Green Waterhole cave sediments: autochthonous calcite crystal and weathered limestone accumulation, likely deposited in submerged conditions, the other allochthonous clays, potentially washing in through the cave entrance. Difficulties in interpretation of the depositional history of this deposit was exacerbated by the inability of scientists in the 1980s to actually observe where exactly samples were taken from, and to not be able to observe the deposit themselves (Newton, 1988). While the use of 3D imagery and video has no doubt alleviated some of these problems (e.g., Schubert et al., 2017), direct, visual, and professional examination of deposits is required so that sites can be interpreted as accurately as possible.

Recommendation 2. Where possible, trained palaeontological divers should directly see, assess, and record the depositional context prior to any planned excavation or fossil extraction.

Recommendation 3. Prior to any disturbance, sites should be as thoroughly and widely surveyed as possible. This should include 3D photogrammetry and video of the deposits themselves, as well as traditional underwater survey methods of the whole site/cave.

Recommendation 4. Sedimentary context should be tested and examined by probing and/or coring fossil-bearing horizons prior to major operations. With this data, areas of interest can be identified and targeted for further excavation or analysis.

Marine caves and continental sites situated underwater now, but dry during glacial periods, also offer unique opportunities to palaeontologists. Reported examples include Stiva Cave, off the coast of Bali, and GNL Quintero 1 in Chile, both of which would have been accessible to fauna and people during much of the Pleistocene. It is highly likely that shallow (i.e., accessible to divers) but currently transgressed continental shelves in other regions will host similar sites. Underwater exploration of the Sunda shelf, for example, has the potential to identify sites that can provide insights into whether savannahs existed during glacial periods in Southeast Asia (Louys and Meijaard, 2010) and how instrumental they might have been for movements and extinctions of hominins and other medium and large-bodied mammals (Louys et al., 2007; Louys and Turner, 2012). The discovery of datable fossils associated with cultural material, for example in the blue hole in the Bahamas and in Page-Ladson in Florida, is an example of the enormous potential of underwater sites for refining chronologies of extinction associated with the arrival of people (Steadman et al., 2007; Webb and Simon, 2006).

While taphonomic studies of flooded deposits are still in their infancy, nevertheless, several studies cited above indicate there are possible taphonomic indicators that could be used to determine whether deposits were flooded when deposited or not, and in the case of the latter, when the flooding occurred. Methods such as recording the orientations of bones, and histological examinations of waterlogged specimens could provide important evidence on site formation. These should be combined with measurements of current environmental conditions such as water pH, temperature, salinity, which will not only provide important data for conservation of the fossils after extraction from water, but may also provide an indication of past environmental conditions. Due to the unique constraints of underwater work, most notably time, taphonomic variables that can be collected from underwater settings will necessarily be less comprehensive than could be achieved in most terrestrial settings. However, with prior planning time underwater can be maximised.

Recommendation 5. More detailed taphonomic studies of both in- and ex-situ fossils from underwater settings are required. The former will necessarily be site specific, but should be planned well before excavation or extraction of fossils is undertaken in an effort to maximise the contextual data that can be collected by divers.

Recommendation 6. Environmental variables of the hosting waterbody should be recorded alongside standard taphonomic variables.

Recommendation 7. Conservation of bones should be planned for before fossils are removed from underwater, and bones should be considered unstable when wet and until such time as conservation and consolidation procedures have been enacted.

While an increase in the number of cave divers can increase the risk that underwater sites might be disturbed, vandalised, or even robbed (González González et al., 2008), it should also be noted that scientific excavation can also inflict long-term damage on sites, as observed in the offshore site GNL Quintero 1 in Chile (López et al., 2016). Ultimately, non-scientific divers, particularly cave divers, have provided much of the initial impetus behind the identification, mapping, and recovery of fossils from underwater settings (Iliffe and Bowen, 2001; Webb, 2006). The research summarised here could not happen without their cooperation, help, and involvement.

Recommendation 8. Carefully evaluate the need to remove bones from the underwater environment. Removal of bones affects not only the fossils and sites, but can detract from the aesthetic appeal and natural beauty of the underwater environment.

Recommendation 9. Technical diving considerations and diving efforts (e.g., total number of dives logged, gas mixtures used, amount of time underwater, total number of divers, etc.) should be reported in the methodology section of any published site report and, where appropriate, divers listed as co-authors. This not only provides important excavation information, but allows for a deeper engagement with the diving community on any given project.

SUMMARY

Underwater palaeontological deposits are most likely to be found in the phreatic zones of caves and near-shore environments of shallow continental shelves. Deposits in underwater caves can accumulate in either already flooded passages, or alternatively once-dry passages can become flooded and existing fossil deposits become inundated. It should be possible to distinguish the two on taphonomic and sedimentological grounds. The former may include representation by complete or almost complete skeletons in anatomical position, but missing autopodia in the case of bloated carcasses later dropping to the cave floor. Sedimentary profiles can include high proportions of carbonate powder and calcite flakes in flooded settings (e.g., Newton, 1988). The action of carnivores, rodents, and potentially root etchings can indicate dry accumulations, although roots are also found underwater. Sedimentary profiles in such scenarios should mimic classic dry cave deposits (e.g., Gillieson, 1996). Taphonomic indices commonly scored for terrestrial deposits can be applied to underwater accumulations, although many of these will only prove informative if the accumulation underwent a 'dry' phase. Furthermore, the very different recovery methods employable in underwater settings will bias any assemblage such that many traditional taphonomic procedures or analyses will not be suitable to any underwater deposits. There is a clear need to develop a specific set of taphonomic variables, observations, and procedures unique to underwater environments. Such analyses will be facilitated by neotaphonomic experiments and observations of modern deposits where possible, and these should be a priority for future research in this field. Deposits found offshore and resulting from marine transgression will largely follow classic terrestrial studies, although the scoring of marine taphonomic processes (e.g., López et al., 2016) also need to be considered.

Most underwater fossil deposits are at a depth and location that makes their recovery very challenging and potentially life threatening. Training and practice of diving in these conditions are necessary before scientific diving is attempted. As such, the palaeontological community will need to continue to rely on the generosity and knowledge of exploratory cave divers, and as such should seek to engage with these communities whenever possible.

Despite many limitations, underwater deposits hold unique advantage relative to dry settings. Because many of these environments have experienced almost no physical or chemical disturbance since flooding, exquisite levels of preservation of fossils are common, with extinct species often represented by complete skeletons in anatomical association. Such deposits provide unparalleled insights into organism palaeobiologies, and many underwater sites should be considered Lagerstätten, with several drowned caves in particular added to the list of Quaternary Konservat-Lagerstätten, of which very few are widely recognised for deposits of this age.

Finally, underwater settings can preserve fossils in regions that might otherwise not have them. For example, on the Yucatan peninsula, Pleistocene sites were unknown until the exploration of sinkholes because the thick limestone bedrock combined with the extremely low topographic relief that limited sediment deposition, dense vegetation, and the high rates of precipitation and humic acids are otherwise unconducive to fossil preservation (González González et al., 2008). Similarly, underwater lake deposits could be an important source of fossils in North America where dense vegetation, moist sediments, and acidic soils inhibit good preservation of bone (Jass et al., 2018). Areas that would benefit from exploration of underwater settings, such as the flooded Sunda shelf in Island Southeast Asia, and otherwise fossil-poor landscapes such as those present in the Yucatan, should be made a priority for future research efforts in this field. Although underwater now, flooded continental shelves in particular provided major corridors of dispersal for terrestrial mammals during glacial periods, including early humans (Bailey and Flemming, 2008). Because these areas are currently underwater, they are almost completely unstudied even though they are critical for understanding the biogeographical histories of regions no longer found today. Underwater sites can provide critical new information on the recent evolution, movement, and extinction of Quaternary mammals not possible in traditional palaeontological settings.

ACKNOWLEDGEMENTS

I'd like to thank two anonymous referees for their insightful comments which helped improve this review, and J. Miszkiewicz and C. Coroneos for helpful discussions on the topic. Thanks to the L. Wilson, P. Getty, and A. Bush for their editorial input. No involvement or conflict of interest from the author existed during the handling of this manuscript. This research was funded by an ARC Future Fellowship (FT160100450).

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