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JOURNAL OF CRUSTACEAN BIOLOGY, 00(0), 1-4, 2015

Journal of Crustacean Biology

'ANCHIALINE' REDEFINED AS A SUBTERRANEAN ESTUARY IN A CREVICULAR OR CAVERNOUS GEOLOGICAL SETTING

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ABSTRACT

An improved understanding of the anchialine ecosystem and geology warrants a redefinition of the term 'anchialine.' Originating from subareal biological observations, the term anchialine now encompasses chemical, physical, geological and biological elements within the subterranean realm. We propose a more accurate definition of the term anchialine as 'a tidally-influenced subterranean estuary located within crevicular and cavernous karst and volcanic terrains that extends inland to the limit of seawater penetration.' This subterranean estuary is characterized by sharp physical and chemical stratification and merges with a marine system at the coast and a groundwater system inland. The anchialine ecosystem supports a relatively diverse biotic assemblage of stygobiotic species of marine origin dominated by members of Crustacea, both numerically and by species richness.

KEY WORDS: anchialine, anchihaline, stygobiotic, subterranean estuary

DOI: 10.1163/1937240X-00002335

HISTORY OF THE TERM "ANCHIALINE"

One of the first reviews in the world of the anchialine fauna was done by Riedl (1966) who introduced the term Randhöhlen (marginal caves), defined mainly on the position and origin of the cave. The anchialine (meaning "near the sea") environment was originally defined as a habitat consisting of "pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides" (Holthuis, 1973). Subsequent documentation of extensive, submerged cave systems by cave-diving explorers and scientists prompted Stock et al. (1986) to update the definition, as follows: "Anchialine habitats consist of 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."

For the past three decades, research in the anchialine environment has expanded rapidly (Sket, 1996; Iliffe, 2000, 2005). International symposia held in 2009 and 2012 unified the understanding of this diverse, but vulnerable ecosystem (Wicks and Humphreys, 2011; Cukrov and Žic, 2012). Classical and genomic-taxonomic descriptions have further cataloged the macro and microbiota inhabiting the anchialine environment (Yager, 1987, 1994; Alcocer et al., 1999; Seymour et al., 2007; Martinez-García et al., 2009; Humphreys et al., 2012; Hoenemann et al., 2013). Geochemical and stable isotope-based studies have described the carbon cycle (Pohlman et al., 1997), nutrient dynamics (Moore, 1999), iodine speciation (Žic et al., 2008), trace metal cycles (Cuculić et al., 2011; Kwokal et al., 2014) and the general (Iliffe,

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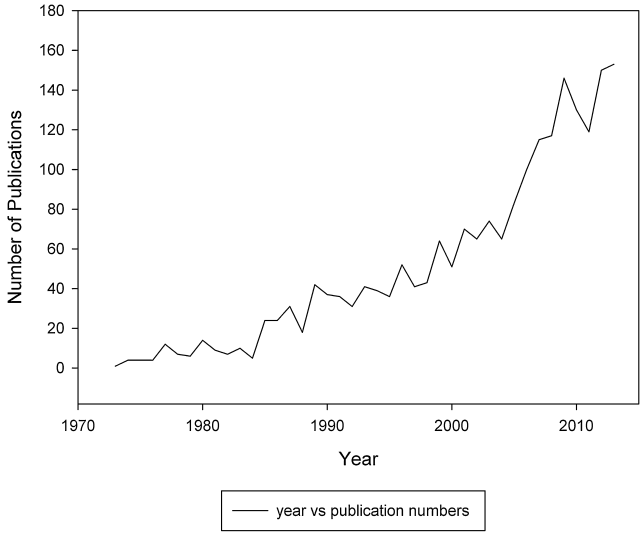

Fig. 1. Publications by year. This figure illustrates the number of publications using "anchialine" or "anchihaline" as a keyword, published per year from 1973 to 2013 in Google Scholar.

2000) and functional ecology (Pohlman, 2011) of anchialine ecosystems. Hydrogeological and paleontological investigations provide models for the short (Beddows et al., 2007) and long-term (van Hengstum et al., 2011) dynamics that have shaped anchialine habitats and recorded external climate-forcing events in the sediment record. The extended definition was associated with a great increase in research on anchialine systems. Prior to the 1986 redefinition, there were 9.2 journal articles per year citing "anchialine" or "anchihaline" as a key word published (1973-1985, $n = 119$), whereas after the definition there was an average of 66 journal articles per year (1986-2013, $n = 1850$; Google Scholar, Fig. 1). In 1987, Holthuis proposed the use of anchialine instead anchihaline based upon frequency of use in the literature, priority and the fact the term does not imply salinity. However, both terms are still widely used and are synonymous. We support the standard use of the term anchialine (pronounced ank^{h}ialaɪn).

Based on our greater understanding of anchialine habitats in general, a round table discussion was convened at the Second International Symposium on Anchialine Ecosystems in Cavtat, Croatia, in October 2012 to reconsider the term 'anchialine.' The panel agreed that a definition orientated within the concept of a 'subterranean estuary,' a term first characterized by Moore (1999) and used in another context as 'groundwater estuaries' as a direct parallel with anchialine systems (Humphreys et al., 2009), would be advantageous.

New Definition of "Anchialine" Proposed

We propose to more broadly define the term anchialine as 'a tidally-influenced subterranean estuary located within crevicular and cavernous karst and volcanic terrains that extends inland to the limit of seawater penetration.'

The anchialine ecosystem supports a diverse biotic assemblage predominantly comprising stygobiotic species of marine origin, many of which are members of higher taxa that are endemic to anchialine habitats and are distinct from those in contiguous limnic and marine waters. This subterranean estuary is dynamic in that it is affected by marine tides; however, dampened tidal fluctuations and isolation from atmospheric turbulent mixing typically yield sharp physical and chemical stratification between the marine and meteoric waters. The anchialine system merges with the marine system at the coast and fresh groundwater inland (Fig. 2). The spatial extent of the system fluctuates in response to the magnitude of groundwater flow and tides, and some 'anchialine' taxa are also found in the contiguous fresh and marine wa-

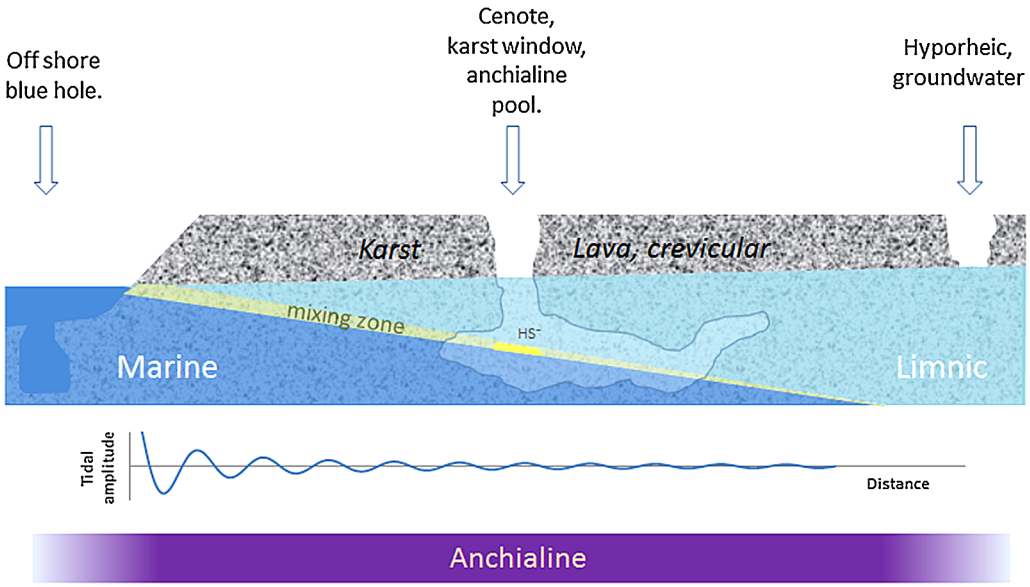

Fig. 2. Schematic outline of the nature and extent of an anchialine ecosystem. The lower bar denotes that some anchialine biota may penetrate marine and limnic habitats. Tidal amplitude decreases with increasing distance from the marine habitat. The mixing zone is thinner with smaller tidal variation, while hydrogen sulphide (yellow) is produced by sulphate reducing bacteria at haloclines in areas of high organic matter input from open sinkholes, such as many cenotes and inland blue holes. This is but the most overt manifestation of the complex and fascinating biogeochemistry of anchialine ecosystems.

ters. Karst windows and submerged cave systems provide portals into anchialine systems.

Anchialine fauna obtain their metabolic energy from surface vegetation either by direct consumption of detrital organic matter, or by trophic transfer of chemotrophic microbes that utilize reduced compounds, e.g., methane and hydrogen sulfide, produced during organic matter degradation (Pohlman et al., 1997; Pohlman, 2011). Some anchialine systems are relatively rich in species and typically support a high proportion of anchialine endemic taxa, especially Crustacea, that dominate the invertebrates both numerically and by species richness (Sket, 1999; Iliffe, 2005; Martinez-García et al., 2009). One class (Remipedia), three orders, nine families, over 75 genera, and more than 300 species are unique to the anchialine environment (Iliffe and Kornicker, 2009). As with stygobionts living in other types of subterranean habitats, the inhabitants of anchialine systems commonly display adaptations to subterranean life in their behavior (Carpenter, 1999; Koenemann et al., 2007), morphology (Boxshall and Jaume, 2000; Iliffe and Bishop, 2007; Koenemann et al., 2008), and biochemistry and physiology (Bishop et al., 2004; Bishop and Iliffe, 2012; Havird et al., 2014; von Reumont et al., 2014).

Our redefinition encompasses all types of pertinent geological contexts (carbonate, volcanic, fractured rock) and accesses (pools, cenotes, blue holes, bores, and caves entered from land or sea).

ACKNOWLEDGEMENTS

We acknowledge the participants in the workshop in Cavtat on 6 October, 2012. In particular, we would like to recognize C. Maier, whose poster at the conference helped get the discussion started. We would also like to thank M. Nakahara for his assistance in providing the correct pronunciation. We also appreciate the input of two reviewers whose efforts served to greatly improve the manuscript.

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RECEIVED: 8 January 2015.
ACCEPTED: 23 February 2015.
AVAILABLE ONLINE: **???**.