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HaloDaSH: The Deep and Shallow History of Aquatic Life's Passages between Marine and Freshwater Habitats

Eric T. Schultz

University of Connecticut - Storrs, eric.schultz@uconn.edu

Lisa Park Boush

University of Connecticut, lisa.park_boush@uconn.edu

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Introduction to “HaloDaSH: The deep and shallow history of aquatic life's passages between marine and freshwater habitats”

Eric T. Schultz^{1, *}

Lisa Park Boush²

¹Department of Ecology and Evolutionary Biology, U-3043, University of Connecticut, Storrs CT 06269-3043; ²Department of Geosciences, University of Connecticut, Storrs CT

*corresponding author: eric.schultz@uconn.edu, 860 486-4692 (tel), 860 486-6364 (fax)

Running title: HaloDaSH: Passages between ocean and freshwater

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Synopsis This series of papers highlights research into how biological exchanges between salty and freshwater habitats have transformed the biosphere. Life in the ocean and in freshwaters have long been intertwined; multiple major branches of the tree of life originated in the oceans and then adapted to and diversified in freshwaters. Similar exchanges continue to this day, including some species that continually migrate between marine and fresh waters. The series addresses key themes of transitions, transformations, and current threats with a series of questions: When did major colonizations of fresh waters happen? What physiographic changes facilitated transitions? What organismal characteristics facilitate colonization? Once a lineage has colonized freshwater, how frequently is there a return to the sea? Have transitions impelled diversification? How do organisms adapt physiologically to changes in halohabitat, and are such adaptive changes predictable? How do marine and freshwater taxa differ in morphology? How are present-day global changes in the environment influencing halohabitat and how are organisms contending with them? The purpose of the symposium and the papers in this volume is to integrate findings at multiple levels of biological organization and from disparate fields, across biological and geoscience disciplines.

Introduction

Marine and freshwater biota have long been intertwined— major branches of the tree of life originated in the oceans and then colonized freshwater habitats. These deep-time halo-transitions had profound macroevolutionary and macroecological impacts: clades diversified, body forms and life histories adapted to the demands of new halohabitats, and biological communities and ecosystems were shaped by the ancestral features and adaptations of the colonists. The fossil record is rich with examples of the transition from marine to freshwater for multiple major taxonomic groups. Yet, these transitions continue as shallow-time processes; contemporary halo-transitions occur in both directions. Indeed, in the shallowest temporal scale for halo-transitions, individual organisms may live in both freshwater and marine environments. The organismal processes that permit halo-transitions, and the contemporary impacts of the transitions, provide an important interpretive context for the deep-time record of biotic change.

A familiar physiological-ecology concept has application in both shallow time and deep time. Euryhalinity is typically viewed as an individual capacity, the ability to tolerate or inhabit a wide range of salinity regimes. Yet it underlies the deep-time processes that shaped the aquatic biota, suggesting that its scope should be broadened from the limits of the individual. Eminent limnologist G. Evelyn Hutchinson (1960) referred to taxa comprising both freshwater and marine members as being ‘evolutionary euryhaline’. He noted that the physiological attributes necessary for “higher organisms” that originated in the ocean to enter freshwater are not uniformly distributed, so that there is a strong phylogenetic signal at higher taxonomic levels for freshwater habitat use.

The symposium “HaloDaSH: The deep and shallow history of aquatic life's passages between marine and freshwater habitats” convened investigators that in aggregate are investigating a diversity of taxa, processes occurring in a range of time scales, and employing multiple approaches. Our aim is to stimulate multidisciplinary research into halohabitat transitions. Investigators who have studied the colonization of freshwater by marine life forms, or vice versa, typically have restricted their analyses to a relatively small portion of life’s diversity. There has also typically been a divide between those examining extant taxa undergoing recent and contemporary change, and those looking at these issues in deeper time. The time is ripe to bridge these divides. Innovations in analysis of paleoenvironmental reconstruction, phylogenetics, genomes, phenotypic evolution and physiological ecology can be brought to bear on long-standing views of aquatic diversification such as those posed by Hutchinson (1960). Exciting theoretical-conceptual progress, such as the recognition of feedbacks between ecological and evolutionary processes, can now guide further work. Furthermore, anthropogenic stressors and their effects differ between freshwater and marine systems; there is an increasingly urgent need to interrogate recent and ancient adaptations to changing aquatic ecosystems to clarify how global change is likely to affect aquatic biodiversity and aquatic ecosystem services.

The symposium was organized to address key themes of transitions, transformations, and current threats. Each theme (Fig. 1) advanced guiding questions. Within the theme of transitions, guiding questions include: When did initial colonizations of freshwaters occur? What physiographic changes facilitated transitions? What organismal characteristics facilitate colonization? Once a lineage has colonized freshwater, how frequently is there a return to the

sea? Within the theme of transformations, guiding questions included: Have transitions impelled diversification? How do organisms adapt physiologically to changes in halohabitat, and are such adaptive changes predictable? How do marine and freshwater taxa differ in morphology? Within the theme of current threats, guiding questions included: How are present-day global changes in the environment influencing halohabitat and how are organisms contending with them? The remainder of this paper will point to how current research is answering these questions, as indicated by papers in the issue, and reflect on how bringing these studies into proximity has underscored important gaps in our knowledge about the biosphere's halo-dash.

Identifying halohabitat transitions

Contributions to the symposium highlighted current understanding of the timing and tempo of halohabitat transitions, which occur as a taxon colonizes a new salinity regime. The deep time history of initial freshwater colonizations, and the global physiographic setting that facilitated these inland transitions, have been interpreted from the Paleozoic fossil record. These initial colonization events left their imprint on upper levels of taxonomies, as is evident in ancestral state reconstructions of the deep nodes in phylogenies: in some taxa, lineages primarily diversified in freshwater after initial colonization and other lineages primarily remained in marine halohabitats. Hence, the boundary between halohabitats has been selectively impermeable, such that it has been breached only rarely. In other taxa the boundary has been relatively porous, transitions have readily occurred in both directions, and the tempo of transitions has been more rapid.

When did major colonizations of freshwaters occur?

The timing and mechanisms of how faunas established themselves within the continental realm is critical to our understanding of clade origination, radiation and derivation throughout time.

Buatois et al. (This issue) draw on multiple disciplines that have been used to reconstruct the gradual pace of Paleozoic continental colonizations. Phyla that eventually established in continental waters were present in marine environments of the Cambrian, and trace fossils indicated occurrence of early Cambrian forays into “coastal environments”, but these pioneers did not establish a sustained enrichment of continental biota. A sustained presence of invertebrate phyla and vertebrates inland occurred after a lag of 100 million years, and higher freshwater taxa continued to arise throughout the Paleozoic as well as the Mesozoic and Cenozoic (Gray 1988; Miller and Labandeira 2002).

Land plants laid the groundwork for freshwater colonization. Establishment of a terrestrial flora in Ordovician and its functional diversification in the Silurian and Devonian conferred changes to landscape, as plants acted as “biogeomorphic engineers” binding sediments, physical stability to continental lotic water bodies. Ecosystems in riparian and adjacent lotic habitats facilitated each other’s maturation. Colonization of freshwater habitats by fishes is evident in the Silurian and Devonian as well, and from forms inhabiting intertidal areas or shallow aquatic habitats arose tetrapods. Distinctive lacustrine ecosystems developed somewhat later in the early Carboniferous. All trophic levels within freshwater systems were established early, but became increasingly complex throughout the Paleozoic. The invasion occurrences and subsequent diversification yielded a dramatically different diversification pattern on continents (e.g. freshwater environments) than in the marine realm (Park and Gierlowski-Kordesch 2007).

What physiographic changes facilitated transitions?

Freshwater faunas likely established themselves through estuarine gateways by multiple invasions during maximum flooding events when ecosystem space expanded on the shelf margin. Groups invading the continents via estuaries did so numerous times via the episodic establishment of marine-freshwater connections along these continental margins. The physiography of Silurian, Devonian, and Carboniferous featured large inland seas, providing ample continental margin contact with brackish and marine waters (Park and Gierlowski-Kordesch 2007). Then, as today, estuaries are gateways to fresh waters. Estuaries feature intermingling of halohabitats, i.e. are rich in salinity gradients, and changing distribution of salinity over various time scales (tidal to long term, as coastline changes). Intuitively these changes offer high opportunities for adapting to new salinity regimes.

Shoreline movements have catalyzed more recent passages of marine fauna into freshwater. Previous work by contributors to the symposium has highlighted the effect of coastline progression on the fish fauna of South America in the Cenozoic. The Neotropical freshwater fish fauna includes multiple taxa with ancestral origins in the Caribbean Sea; the timing of colonization episodes is coincident with marine incursion events, i.e. shoreline progression (Bloom and Lovejoy 2017; Fontenelle and others 2021). Retreat of the shoreline has also catalyzed freshwater diversification of taxa in transition from marine waters. Threespine stickleback populations that were anadromous, i.e. migrating between marine and freshwaters for reproduction, became isolated in freshwater habitats because of isostatic rebound occurring as Pleistocene glaciers melted. The subsequent adaptation to freshwater halohabitat upon

landlocking has furnished classic studies in rapid evolution of morphology, physiology and behavior (Aguirre and others This issue).

What organismal characteristics facilitate colonization?

The estuarine gateway is a selectively permeable barrier through which some taxa have not passed. Some marine phyla have no freshwater lineages (as noted in Okamura and others This issue). Hutchinson (1960) described the ability of metazoan taxa to invade freshwater as “irregular and probably represent[ing] a statistically superdispersed system” resulting from physiological tolerances that represented pre-adaptations for freshwater life. Okamura et al. (This issue) review features of parasitic organisms that are likely to facilitate colonization with their hosts of new halohabitats. Thus, a parasite that is ideally pre-adapted for transition is a generalist endoparasite that is trophically transmitted and has a simple life cycle.

Populations that are able to colonize a new halohabitat are expected to have attributes promoting tolerance of disturbance and euryhalinity. Tolerance of brackish water must be a prerequisite for passage between marine and freshwaters, and habitats with brackish waters (i.e. estuaries) undergo predictable and unpredictable fluctuations on multiple time scales.

Populations that can maintain themselves in such habitats are resilient as a result of relatively robust plasticity, and/or have high allelic diversity maintained by balancing selection on genotypes (Lee 2016; 2021). Similarly, gene duplication played a key role in promoting transition to freshwater in some groups (Horn and Anderson 2020; Horn and others 2019).

Successful colonizers should also be those with life history attributes facilitating rapid expansion into new habitat, such as high fecundity and short generation time (Lee and others This issue).

Once a lineage has colonized freshwater, how frequently is there a return to the sea?

Freshwater taxa would seem to have ample opportunity to drift, crawl or swim downstream to colonize the sea. Yet among ray-finned fishes, there has been a pronounced bias towards marine-to-freshwater transitions (Betancur-R and others 2015). Hence, the shifting estuarine gateway between marine and freshwater may be in some cases a barrier to transitions like a turnstile that more readily allows passage in one direction than another. Some turnstiles, such as the one imagined for diatoms (which had been likened to Julius Caesar's army "crossing the Rubicon", an exemplar of auspicious irreversibility), have been dismantled by more-detailed phylogenetic analysis (Alverson and others 2007) suggesting that there has been a comparable number of successful colonizations. Finally, some groups show a bias towards colonization of marine waters from freshwaters, as shown by Okamura et al. (Okamura and others This issue) in their analysis of transitions by parasites.

Documenting biotic transformations

Have transitions impelled diversification?

Transitions to novel habitats and the occupation of new ecospace often give rise to diversification. The colonization of freshwaters indeed stimulated a great deal of cladogenesis, as reflected in the apportionment of diversity across halohabitats. Theory predicts that diversity should increase with the size of the habitat and the period of time that the habitat has been occupied. Given these considerations the diversity of freshwater halohabitat should be dwarfed by the diversity of marine habitats. Yet the profile of biodiversity with respect to salinity, known as the Remane curve (Remane and Schlieper 1971) is roughly U-shaped. The

“freshwater paradox” challenges us to identify the factors that initiated and have sustained the disproportionately high diversity of freshwater systems. One approach that is increasingly being applied in this inquiry is the application of phylogenetic methods to compare the rates of speciation and extinction in lineages occupying different halohabitats (Nakov et al 2019, Betancur et al. 2015, Bloom et al 2013, Miller 2021, Roman-Palacios et al 2022). These analyses are clarifying when, where and in what groups the net diversification of freshwater halohabitats has exceeded that in marine systems.

An analysis reported in this issue (Davis and others This issue) yields a nuanced result that tempers hopes for simple generalization about the extent to which there are halohabitat differences in diversification. Following up on a previous finding of higher net diversification rates in freshwater within a group of shrimp (Davis et al. 2018), the authors broadened the scope of the analysis to Decapoda. They combined phylogenies across the order, constructing a ‘supertree’ upon which they performed ancestral state reconstruction of halohabitat. Four groups of Decapods enable SW-FW comparison. In all four, the median estimated speciation rate in FW exceeds that in SW and quartiles do not overlap. Yet over all Decapoda there is no discernable difference in speciation rate between halohabitats, because high rates of diversification have occurred in some lineages confined to marine habitats. While a typical value for speciation rate in marine systems has been 0.02-0.03 species over a million years, one marine-only taxon, Polychelida, has a high rate of almost 0.1. This is about equal to the highest freshwater speciation rate, which is seen in Brachyura. Polychelida appears to represent a case of diversification upon transition in a direction *away from* land: extant members are deepwater

burrowing forms believed to have descended from a shallow epibenthic ancestor (Ahyong 2009).

Many factors could modulate diversification rate, among them ecological interactions. Adaptive radiation, in which diversification is rapid because of expansion into available niche space, is impelled by competitive interactions and character displacement. At the same time, competitive interactions can impede diversification upon colonization because niche space is occupied by incumbents, i.e. taxa that are already present in the newly colonized habitat. The latter scenario is illustrated by ariid catfishes, which colonized freshwaters independently on multiple continents (Betancur et al. 2012). An inverse relationship between the number of ariid species that remain from each colonization episode and the current species richness of fishes other than ariids at the site suggests that competition by incumbents limits opportunity for diversification of colonists. Freshwater stingrays in South America offer a counterexample, in which regional incumbent species richness has not inhibited cladogenesis of the colonist (Kolmann et al., this issue).

How do organisms adapt physiologically to change in halohabitat, and are such adaptive changes predictable?

Determining the organismal traits necessary for clades to invade continents allows us to better characterize the nature of these invasions and understand the requirements for survival and reproduction in freshwater environments as well as informing on the possible cause of diversity disparity across the tree of life. A wide array of biotic and abiotic challenges confront such colonists. Similarly, a freshwater lineage would face multiple challenges to colonizing the marine habitat. Foremost among the challenges of transitioning is, of course, that the

abundance of solutes and hence available water differs substantially, and the greatest attention has been paid to how osmoregulatory physiology has adapted. (In contrast there has been relatively little progress on adaptation to environmental factors that differ between continental and marine waters, such as temperature or energy availability). Physiological systems respond to transitions in halohabitat on multiple time scales, from acute responses to acclimatory responses (see e.g. Downey and others 2022; Judy and others 2022 for dissection of acute and acclimatory responses of diatom via transcriptome analysis), to heritable changes that appear in comparing the acute and/or acclimatory responses of multiple lineages. Inquiries into these responses can be conducted by confronting organisms with a salinity challenge and testing endpoints on multiple hierarchical levels, from transcriptional and cellular responses up to whole-organism performance metrics such as survival and measures of osmoregulatory homeostasis (see e.g. review by Schultz and McCormick 2013 on diversity among rayfined fishes in salinity tolerance and physiological adaptations).

The locus and means of homeostatic control in the face of changing salinity vary in several general ways among organisms. Invertebrates that are able to live in complete freshwater for their entire life cycle (i.e. are hololimnetic) maintain a osmolality differential between their body fluid and the environment via salt uptake and water elimination. McNamara and Freire (this issue) review general strategies of hololimnetic invertebrates. Some groups such as decapod crustaceans maintain high levels of osmolality, in comparison to molluscs, annelids, rotifers and cnidaria. This approach is variously facilitated by larger body size and thus low surface area to volume, a low permeability cuticle, and further modifications of intercellular junctions in gill epithelia to reduce passive leakage of ions. There is also notable variability

among groups in their range of halotolerance; some hololimnetic crustacea are tolerant of full seawater and can even hypo-osmoregulate, i.e. maintain body fluid concentrations lower than that of their environment. The review of McNamara and Freire (This issue) underscores that broadly similar approaches to freshwater adaptation have appeared multiple times independently, that these strategies are relatively understudied in taxa other than the arthropods, and that the evolutionary history by which these strategies have arisen remains to be explained.

Among lineages in large taxa, physiological transformations upon transition to new halohabitats may follow parallel paths, with similar mechanisms of adaptive change at genomic, cellular, tissue, and organismal levels. Adaptive changes in response to halohabitat change should be relatively predictable, in comparison to responses to other environmental change such as temperature (Lee and others This issue). The degree to which there have been parallel physiological changes upon transition in halohabitat in teleost fishes at the genomic level has been tested by Velotta et al. (This issue). Teleosts are osmoregulators, hence are capable of hyperosmoregulating in freshwater and hypo-osmoregulating in seawater. The means by which they osmoregulate are fairly well understood and are similar across the clade, and as such osmoregulatory adaptive change may be highly repeatable. This should be evident in comparisons of genomic data of fish species that have evolved into different halohabitats as has arisen, for example, when an anadromous species has become landlocked in some places and hence has specialized on the freshwater halohabitat. Velotta et al. (This issue) assembled genomic data from multiple such cases and tested whether genes or gene families functioning in osmoregulation repeatedly exhibited signatures of selective evolutionary change across the

salinity boundary. They found that selective changes are widely distributed across genes that function in ion exchange, so that the gene-level signature of adaptive change is rather idiosyncratic to each species that independently has adapted to new halohabitat. Nonetheless, a test that grouped genes into families representing functional pathways revealed that several such gene families are repeatedly targets of selection. Two of the gene families that have repeatedly been targets of selection are ion pumps (ATPases), which may be expected given the unique role they play in powering ion exchange. A third gene family that is repeatedly been subjected to selective change is a poorly understood membrane channel; this finding highlights that genomic-level analyses have an unmatched potential to discover gaps in our understanding that now can be attacked with functional studies.

How do marine and freshwater taxa differ in morphology?

The sharp ecological changes that lineages undergo upon transition to new halohabitats provide excellent opportunities to test theory in evolutionary ecology. High diversification rates, as have been found in some cases (see above) indicate that transitions, with concomitant expansion of ecological opportunity, have the potential to initiate episodes of adaptive radiation. Yet the degree to which morphology diversifies may be restrained by niche conservatism, and should be mediated by competitive interactions with incumbent and co-colonizing taxa. Papers in this series offer insightful case studies using phylogenetically explicit methods in how functionally-important features of fish bodies are (or are not) affected upon colonization of and diversification in freshwater over macroevolutionary timescales. A complementary perspective is provided with a paper that focuses on contemporary microevolutionary change occurring in Threespine Stickleback, enabling finescale determination

of genetics underlying rapid evolutionary change and convergent evolution among recently colonists of freshwater.

Kollman et al. (This issue) evaluate the tempo and timing of diversification in trophic morphology and diet in a group of stingrays that colonized freshwater in South America. The timing of this colonization, the group giving rise to it, and the conditions promoting it have been well worked out (see above). In the paper in this issue, analysis turns to ecomorphological diversification. The ancestral form from which the colonizing group was derived had a generalist body form likely to have consumed fish and benthic invertebrates. From it, a piscivore lineage appeared early after colonization, and subsequently other specialized forms evolved, including a repeatedly-evolved specialization on insects that is unique to cartilaginous fishes. A burst of trophic structure diversity erupted when this specialization and another specialization on gastropods arose. Overall, the freshwater stingrays of South America represent a case of diversification that is not particularly constrained by niche conservatism or competition by incumbent fishes.

De Brito et al. (This issue) focus on evolutionary changes in body size. Earlier studies on individual clades suggested that transition to freshwater causes reduction in size (Bloom and others 2020; Davis and others 2014; Kolmann and others 2020) and diversification in body form (Betancur-R. and others 2012; Davis and others 2014). However, phylogenetic comparative analysis of data from nine clades (de Brito and others This issue) does not support the hypothesis that halohabitat transitions impel characteristic shifts in size, nor that increase in ecological opportunity upon transition stimulates diversification in size. There is also no support for the restraining influence on diversification of competition from the incumbent fauna. As is

also suggested in Kollman et al. (This issue), phenotypic diversification of colonists may be neutral to or may be stimulated by potential competition from incumbents. Intriguingly, the diversity of “closely related species in the same region” does have a restraining influence on body size diversification, perhaps reflecting an inverse relationship between speciation rate and niche lability. The findings of de Brito et al. (This issue) have a similar takeaway to those of Davis et al. (This issue), tempering hopes for easy generalization. It remains unclear whether, as de Brito et al. (This issue) suggest, transitions between marine and freshwaters do not represent changes in ecological opportunity, or alternatively that body size is not a reliable indicator of a fish species’ niche.

Freshwater populations derived from ancestral marine or anadromous forms continue to be founded in the present day, by natural or anthropogenic means. Aguirre et al. (This issue) provide an update on the decades-scale changes that have been observed since several lake populations of Threespine Stickleback were founded by anadromous forms. It is now well known that isolated freshwater populations of this species have arisen from marine and anadromous ancestral forms for millions of years and that a multitude of existing lake populations throughout the Holarctic have been founded since Pleistocene deglaciation. Highly replicated, these freshwater forms have changed from the ancestral marine form in a remarkably predictable fashion, because freshwater-adapted genotypes are assembled from alleles for freshwater phenotypes that are present throughout the genome in the marine and anadromous forms (and hence the colonists) at low frequency. This process is now being observed in contemporary time, revealing a startling rapid and predictable mode of evolutionary change. Within a few decades, newly-established lake populations have

undergone rapid change in regions of the genome associated with freshwater adaptation, and have nearly completed convergence on a classic freshwater phenotype.

Assessing current threats

Mitigation and adaptation to global change require an exhaustive analysis of anthropogenic stressors and a thorough understanding of how natural systems respond to them. Aquatic systems are subject to a common set of familiar anthropogenic stressors, including eutrophication, acidification, warming temperatures, habitat alterations, and overexploitative harvesting. Lee et al. (This issue) focus on salinity change, which is a globally-extensive stressor on both marine and freshwater systems that has not been well documented. While a more systematic monitoring network has not yet been implemented, it is clear that ocean waters at high latitudes are becoming fresher (see also Pinseel and others 2022), whereas at low latitudes they are becoming more saline. Continental waters in some areas are becoming more saline as a result of land use practices, road salt application and sea level rise. The impact of these changes on biotic systems will depend on the capacity of the organisms to acclimate and adapt, thus there is a critical need to understand how physiological systems cope with varying salinity and the extent of genetic variability capable of responding to selection on these systems. Empirical investigations of these responses must also be attentive to interactions with other factors, such as temperature, that are also changing. Geographical ranges will doubtless continue to shift in response to anthropogenic global change, and the degree to which changes in salinity regime are shaping these range shifts is quite unclear because of an inadequate understanding of the salinity dimension to the ecological niche. Lee et al. (This issue) express a call to action that includes more comprehensive monitoring of salinity, a more thorough

understanding of organismal and population responses to salinity change, and improved ability to project range shifts through ecological niche modeling.

Concluding remarks

This introduction has mainly reviewed each paper in the series as a distinct contribution, but their topics are connected and flow into one another, as Figure 1 implies. Paleontological findings such as those described in Buatois et al. (This issue) provide context and chronology for transitions and associated diversification in clades such as described in Davis et al. (This issue) and Okamura et al. (This issue). Differences and similarities in halotolerance and physiological responses to salinity (e.g., McNamara and Freire This issue) illuminate the filtering process that shapes the macroevolutionary patterns. The genes and gene families that have evolved under selection, sifted from the genome by approaches such as those by Velotta et al. (This issue), also indicate the organismal functions that are adaptively altered in colonists. These, along with morphological changes (Aguirre and others This issue; de Brito and others This issue; Kolmann and others This issue), can signify innovations enabling occupation of new ecospace and adaptive radiation. Only with the insights provided by these studies of deep time and shallow time transitions can there be informed approaches to managing the impact of anthropogenic stressors to aquatic systems (Lee and others This issue).

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Figure Caption

Fig. 1. Themes and topics covered by papers in this series.

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