Environmental Variation, Life History Attributes, and Community Structure in Stream Fishes: Implications for Environmental Management and Assessment

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ABSTRACT / Fishes in midwestern streams of the United States experience strong upstream–downstream gradients in natural environmental variability. Upstream fishes experience greater temporal variability in physical–chemical conditions than downstream fishes, particularly in intermittent streams. Associated with these changes in environmental variability, basic changes occur in life history attributes and temporal variation in community structure of stream fishes. As a whole, upstream species have a shorter life-span, smaller body size, and earlier sexual maturity than downstream species. Descriptive studies also suggest upstream species exhibit more rapid recolonization after severe physical disturbance than downstream species, and fish community structure is temporally more variable in upstream than downstream areas. These longitudinal differences in life history characteristics suggest that upstream fish communities will exhibit more rapid recovery from severe anthropogenic disturbances than downstream fish communities. The greater temporal variability of fish community structure in upstream areas also suggests it will be more difficult in upstream than downstream areas to use fish-based indices to distinguish whether subtle changes in environmental quality are due to natural or anthropogenic disturbances. Long-term monitoring of fishes throughout drainage basins is critically needed to establish more precisely the natural range of variation in community structure. Such monitoring will allow regulatory agencies to distinguish, with greater confidence, the influence of anthropogenic disturbances on stream fishes from the influence of natural environmental variation.

Stream fish ecologists have long recognized the effect of both abiotic (Starrett 1951, Larimore and others 1959, Horwitz 1978, Coon 1987, Finger and Stewart 1987) and biotic (Mendelson 1975, Power and Matthews 1983) factors on stream fishes. However, there have been few attempts to integrate how the relative influence of these factors changes longitudinally along streams and, perhaps more importantly, the implications of these changes for environmental management and resource assessment procedures. In light of this, my objectives are, first, to summarize briefly the patterns of upstream–downstream environmental variation in natural lotic ecosystems. I then illustrate how life history characteristics and temporal variation in community structure of fishes changes along upstream–downstream gradients. Finally, I examine the implications of these results for the potential rate of recovery of upstream vs downstream fish communities from anthropogenic disturbances and the current use of fishes to monitor resource degradation from these disturbances.

KEY WORDS: Anthropogenic; Community structure; Disturbance; Environmental management; Environmental variation; Index of biotic integrity; Life history characteristics; Longitudinal variation; Recovery from disturbance; Stream fishes

Environmental Gradients in Streams

Three interrelated environmental variables in streams are likely to have major effects on life history characteristics and temporal variation in community structure of fishes. These include flow regime, channel morphology, and physical–chemical attributes (e.g., temperature and oxygen).

Flow Regime

Flowing water is the fundamental attribute of lotic ecosystems, having profound effects on physical, chemical, and biological characteristics (Hynes 1970, Fisher and others 1982, Schlosser and Ebel 1989). Stream discharge originates as the output from the terrestrial component of the hydrologic cycle via one of four pathways: Horton overland flow, saturation overland flow, subsurface flow, and groundwater flow (Dunne and Leopold 1978). The relative importance of these pathways changes among drainage basins because of historical differences in climate and geology that affect vegetative cover, infiltration rate, and subsurface storage capacity (Dunne and Leopold 1978). Horton overland flow predominates in basins with low infiltration rates and/or low subsurface storage capacities. These runoff-fed streams exhibit accentuated high- and low-flow conditions. In basins with high infiltration rates and/or subsurface storage capacities, subsurface or groundwater flow predominates. These streams have less extreme high- and low-flow conditions.

Similarly, because of their coalescing nature, streams exhibit considerable upstream–downstream differences in discharge patterns. Upstream areas experience accentuated low-flow conditions but their floods are smaller and of shorter duration. Downstream areas experience less accentuated low-flow conditions but larger and more prolonged floods (Dunne and Leopold 1978).

A comprehensive analysis of variability in stream flow was conducted by Horwitz (1978). He examined coefficients of variation in discharge from long-term records for 15 river systems, including runoff-fed, groundwater-fed, and spring-fed rivers. Generally, variability in flow was higher in upstream than downstream sections and higher in runoff-fed than groundwater-fed and spring-fed rivers.

Variability in stream flow has the potential for both indirect and direct effects on fishes. Indirect effects include alteration in habitat suitability, nutrient cycling, production processes, and food availability (Stalnaker 1981, Elwood and Waters 1969, Fisher and others 1982, Schlosser and Ebel 1989). Direct effects include decreased survival of early life history stages (Starrett 1951, Muncy and others 1979, Schlosser 1985, Finger and Stewart 1987) and potentially lethal temperature and oxygen stress on adult fishes (Larimore and others 1959, Tramer 1978).

Channel Morphology

The three-dimensional morphology of the stream is the templet upon which most biological processes occur (Southwood 1977, Vannote and others 1980). The morphology of the channel is created by the energy flux associated with discharge of water and particulate materials from the drainage basin (Curry 1976). As water flows through the stream, its energy is transformed from potential to kinetic energy. This transformation provides the energy for erosion and transport of sediment. Since the transformation from potential to kinetic energy is governed by the second law of thermodynamics (Leopold and Langbein 1962), it results in the creation of predictable patterns of channel morphology, including meandering, concave longitudinal profiles, and pool–riffle bedforms (Leopold and others 1964, Langbein and Leopold 1966, Yang 1971). Pools, which are particularly critical for stream fishes, are formed by scouring processes during bankfull flow (Keller 1977). Since the amount of kinetic energy available for scouring is primarily dependent on the mass of the water (Keller 1977), pools tend to be small and shallow in upstream areas but large and deep in downstream reaches.

Large pools are important for stream fishes because they provide refugia from both harsh physical conditions and certain types of predators. Large pools reduce the effect of low stream flow on temporal variation in habitat volume (Schlosser 1982a), temperature (Neel 1951), and dissolved oxygen (Harrell and Dorris 1968). Similarly, they provide stable refugia during harsh winter conditions when ice-over and reduced flow can restrict habitat availability (Toth and others 1982). Finally, terrestrial predators, such as herons, are effective when foraging in shallow habitats, whereas pools provide refugia from this risk of predation (Power 1987).

Physical–Chemical Factors

Two physical–chemical factors are likely to be important to stream fishes: temperature and dissolved oxygen. Stream temperature is controlled primarily by the amount and temperature of the groundwater, surface exposure to solar radiation, and volume of the water being heated (Vannote and Sweeney 1980). If there is sufficient influx of groundwater in headwater areas and riparian vegetation is present, temporal variation in stream temperature is highest in midriver reaches (Vannote and Sweeney 1980). The normal magnitude of this variability (6–8°C) is unlikely, however, to exceed the thermal tolerance of most fish species and in fact may be necessary to initiate spawning in warm-water taxa (Becker 1983). However, if stream flow is intermittent, pool volume small, and riparian vegetation poorly developed or absent, then high temperatures (35–40°C) can occur in headwater streams, directly causing mortality of fishes (Larimore and others 1959, Harrell and Dorris 1968).

Oxygen levels in streams are primarily a function of the balance among photosynthesis and respiration, water temperature, water volume, and reaeration of the stream by turbulence. Flowing streams usually have sufficient mixing to maintain adequate oxygen for fishes, even in upstream areas. However, if intermittent flow occurs, particularly in conjunction with leaf decomposition and high temperatures, then low (<1 ppm) oxygen levels can result in fish mortality (Larimore and others 1959, Tramer 1978).

Interspecific Variation in Life History Characteristics of Fishes along Environmental Gradients

To illustrate the association between these environ-

Table 1. Taxonomic characterization of headwater (HW), midriver (MR), and large river (LR) fishes in the Illinois River Basin, Illinois[a]

	Number of species		
Family	HW	MR	LR
Acipenseridae	—	—	2
Polydontidae	—	—	1
Lepisosteidae	—	1	3
Clupeidae	—	—	2
Hiodontidae	—	—	2
Esocidae	—	2	—
Cyprinidae	18	13	6
Catastomidae	2	8	5
Ictaluridae	2	6	3
Cyprinodontidae	2	—	1
Gasterosteidae	1	—	1
Cottidae	2	—	—
Percicthyidae	—	—	2
Centrarchidae	2	9	3
Percidae	8	7	2
Other Families	4	6	3
Total	41	52	36

[a]Habitat classification based on Karr and others (1983).

mental conditions and life history attributes of fishes, I compared select life history characteristics of fishes in upstream vs downstream areas of the Illinois River, Illinois, USA. One hundred twenty-nine species found in the Illinois River (Table 1) were categorized as either headwater (first–third order; 41 species), midriver (fourth–sixth order; 52 species), or large river (seventh–twelfth order; 36 species) species based on the information in Karr and others (1983). Life-span, maximum body size, and age at sexual maturity were estimated for each species using regional fishery texts (Pflieger 1975, Smith 1979, Becker 1983). Age specifications followed the standard convention, where age I fish were those surviving one winter, age II fish surviving two winters, and so on. Since fish are somewhat plastic with respect to life history characteristics, and the range of values in the literature for some life history traits was large, fish were only placed into general categories for each trait. To test whether life history characteristics of headwater, midriver, and large river species were dependent on their stream position, an $R \times C$ test of independence, using the G statistic and Williams correction (Sokal and Rohlf 1981), was conducted for each life history trait.

Maximum life-span ($G = 49.09$; $P < 0.001$) and maximum body size ($G = 57.03$; $P < 0.001$) of fish species in the Illinois River were both dependent on stream size (Figures 1 and 2). Headwater species exhibited a strong modal value of III–IV years maximum life-span. Midriver and large river species did not exhibit as strong a modal value, and numerous species lived longer than VI years, with several living as long as XX–XXV years. Variation in maximum body size of fish species, as indicated by standard length, exhibited a similar, strong increase in midriver and large river species (Figure 2). Eighty percent of the species in headwater streams had a maximum body size <200 mm. In contrast, only 40% of midriver and 20% of large river species had a maximum body size <200 mm. No headwater species had a maximum body size >400 mm, while 35% of midriver and 70% of large river species had a maximum body size >400 mm.

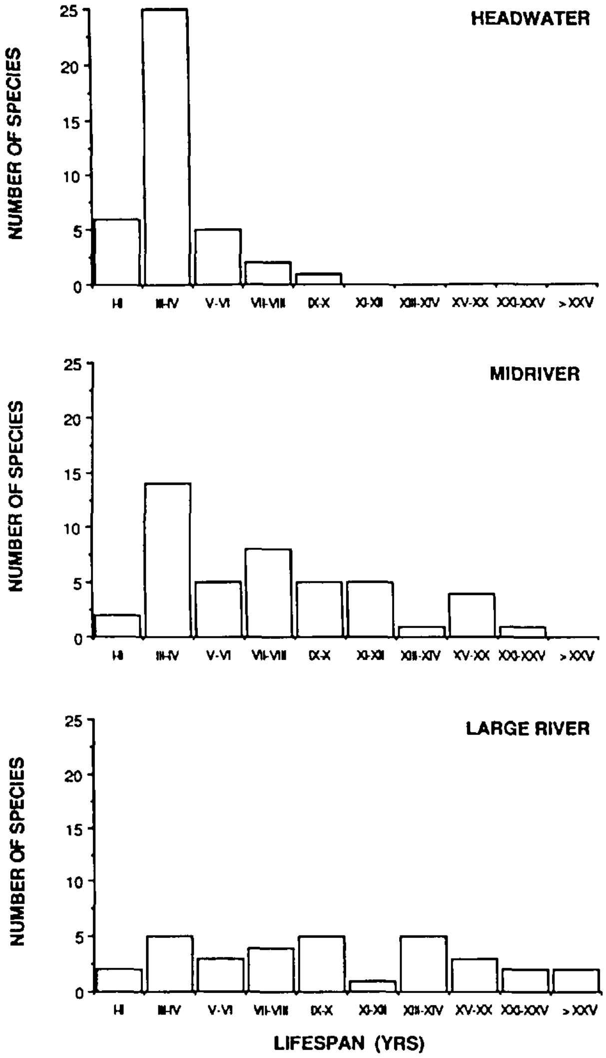

Figure 1. Life-span (years) for headwater (39 species), midriver (45 species), and large river (32 species) fishes occurring in the Illinois River, Illinois. See text for explanation regarding source of data and definition of stream types.

Age at sexual maturity of the fish species also was dependent ($G = 36.08$; $P < 0.001$) on stream size

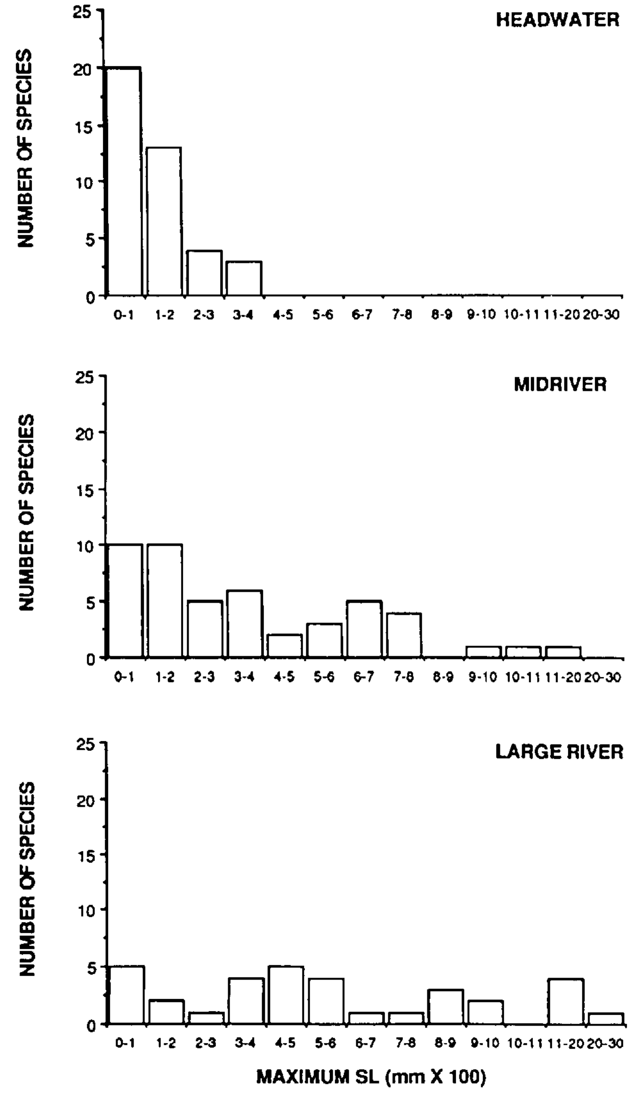

Figure 2. Maximum standard length (SL) for headwater (40 species), midriver (47 species), and large river (33 species) fishes occurring in the Illinois River, Illinois.

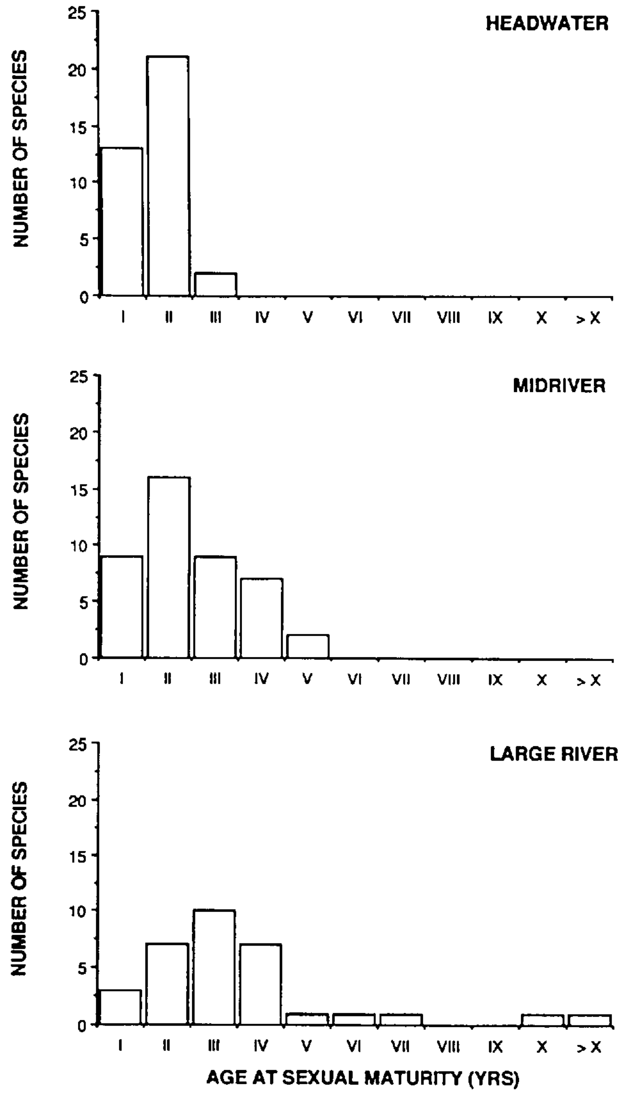

Figure 3. Age at sexual maturity for headwater (36 species), midriver (43 species), and large river (32 species) fishes occurring in the Illinois River, Illinois.

(Figure 3). However, the increase was not as dramatic as the increase for longevity and maximum body length. Modal value for sexual maturity was age II in headwater and midriver species but age III in large river species. Ninety-four percent of headwater species were mature by age II, while only 58% of midriver and 31% of large river species reached maturity by this age.

Temporal Variation in Fish Community Structure along Environmental Gradients

Temporal variation in fish community structure also differs considerably along upstream–downstream environmental gradients. To illustrate this, I briefly summarize patterns of fish density, species richness, and species density along an upstream–downstream gradient in Jordan Creek, a second-order stream in east-central Illinois.

Three distinct stream reaches occur along Jordan Creek based on the channel morphology and longitudinal position of the reaches, including: (1) a low-gradient (0.65 m/km) modified upstream reach with uniform shallow habitats created by channelization, (2) a moderate-gradient (0.95 m/km) natural upstream area with well-developed small pools and riffles, and (3) a high-gradient (4.0 m/km) natural downstream area with large rocky riffles and well-developed pools. Normally, three 100-m reaches were sampled in each of the upstream areas and five 100-m reaches were

Table 2. Mean and coefficient of variation (in parentheses) of fish density (N/100 m^2), species richness (N species/100-m sampling station), and species density (N species/100 m^2) in three regions of Jordan Creek, Illinois[a]

Community attribute	Modified upstream	Natural upstream	Downstream
Fishes	109 (108)	142 (57)	36 (19)
Species richness	12 (18)	18 (18)	19 (5)
Species density	3.0 (32)	4.3 (21)	2.9 (8)

[a]Adapted from Schlosser (1987b). See text for details.

sampled in the downstream area. Fish were sampled eight times over a two-year period with a combination of minnow seines and electric seines (see Schlosser 1982a, 1987b for details).

Fish density (number per 100 m^2) tended to increase from the modified to natural upstream area and decrease in the downstream area (Table 2). The downstream decrease in fish density was associated with an increase in the abundance of large piscivores (Schlosser 1987b). More importantly, there was substantial temporal variation in fish density, but the variation was not equal among regions (Table 2). A comparison of coefficients of variation in fish density over the two-year sampling period, based on ratios of the variance in logarithms of the measurements (Lewontin 1966), indicated the two upstream areas did not differ ($P > 0.05$) in temporal variability of fish density, but fish density in both upstream areas was more variable ($P < 0.05$) than in the downstream area. Greater temporal variability of fish density in upstream areas was attributable to two components: greater seasonal variation and greater annual variation (Schlosser 1987b). Greater seasonal variation of fish density in upstream areas was due to decreased abundance of fishes after winter and increased abundance of juvenile fishes in late summer and autumn (Schlosser 1982a,b, 1987a). Greater annual variation of fish density in upstream areas was associated with annual variation in juvenile recruitment, which was strongly influenced by annual variation in stream flow (Schlosser 1985).

Species richness (number of species per 100-m station) usually increased from modified to natural upstream areas but was similar in natural upstream and downstream areas (Table 2). In contrast, species density (number of species per 100 m^2) tended to be highest in natural upstream habitats (Table 2). More importantly, substantial temporal variation occurred in both species richness and species density but, again, the degree of variation was not equal among regions (Table 2). A comparison of coefficients of variation in species richness and species density over the two-year period indicated that the two upstream areas did not differ ($P > 0.05$) in temporal variability, but both upstream areas were more variable ($P < 0.05$) than the downstream area. Greater temporal variation in upstream areas was associated with low species richness and species density after winter and high species richness and species density in late summer and autumn (Schlosser 1987b).

Implications for Environmental Management and Resource Assessment

In summary, upstream and downstream areas of midwestern lotic ecosystems exhibit substantial differences in natural environmental variability, fish life history characteristics, and temporal variation in fish community structure (Table 3). These differences have considerable implications for the potential recovery rate of upstream vs downstream fish communities from anthropogenic disturbances and our ability to distinguish whether temporal changes in fish community structure are due to natural or anthropogenic causes.

Upstream areas exhibit small pool refugia and substantial temporal variation in physical–chemical characteristics, especially in streams with intermittent flow (Table 3). In contrast, downstream areas, particularly in the main channel, exhibit large, well-developed pool refugia and less temporal variation in physical–chemical characteristics.

Associated with these longitudinal environmental changes, upstream and downstream species exhibit dramatic differences in life history characteristics (Table 3, Figures 1–3). As a whole, upstream species have a shorter life-span, smaller maximum body size, and earlier sexual maturity than downstream species. In addition, upstream fishes also seem to exhibit more rapid recolonization after severe disturbances than downstream fishes. For example, Larimore and others (1959) monitored fish abundance in Smiths Branch, Illinois, before and after the fish community was totally decimated by a drought. Postdrought samples were collected 13–14 weeks after stream flow resumed. Families typical of upstream reaches, including Cyprinidae and Percidae (Table 1), were more abundant after the drought, suggesting rapid recolonization of the stream by these species. In contrast, fami-

Table 3. Summary of environmental conditions, fish life history characteristics, and temporal variation in fish community structure along longitudinal gradients in midwestern streams

Variable	Upstream	Downstream
Environmental conditions	Small pool refugia; temporally variable, especially in intermittent streams	Large pool refugia; temporally stable
Life history	Short life-span, small body size, early sexual maturity; rapid colonizers	Long life-span, large body size, late sexual maturity; slow colonizers
Hypothesized recovery rate from anthropogenic disturbance based on life history traits	Fast	Slow
Temporal variation in community attributes	High	Low
Confidence limits on indices of resource degradation	Broad	Narrow

lies typical of downstream areas, including Centrarchidae and Catastomidae (Table 1), had not reached predrought abundances 14 weeks after resumption of flow, suggesting slower recolonization by these species.

Thus, based strictly on life history and recolonization characteristics of their respective faunas, upstream fish communities are likely to exhibit more rapid recovery from severe anthropogenic disturbances than downstream fish communities. Fish communities in large rivers will potentially take 20–25 years to reestablish predisturbance age/size structures. The actual rate of recovery from a severe disturbance will, however, depend on numerous other geomorphological and biological factors identified in other papers in this symposium (e.g., Cairns 1990, Gore and Milner 1990). To understand how these variables interact with life history characteristics to determine ultimate recovery rates will require controlled experimental disturbances in both upstream and downstream areas.

Basic differences in temporal variability of fish community structure also occur along streams (Table 3). In upstream areas, frequent effects of climatic variation, such as harsh winter conditions and fluctuations in stream flow, result in a temporally variable fish community structure (Table 3). In contrast, effects of climatic variation seem to be relatively infrequent in downstream areas, resulting in a relatively stable fish community structure.

This longitudinal pattern of temporal variability has considerable implications for using fish-based indices, such as the index of biotic integrity (IBI) (Karr and others 1985, 1986), to assess the extent of resource degradation resulting from anthropogenic disturbances. Since IBI detects temporal variation in fish community attributes as a result of natural environmental variability (Karr and others 1987), the index exhibits broader confidence limits in upstream than downstream areas (Table 3). For example, standard deviations of IBI in upstream Jordan Creek are two to three times larger than those for downstream Jordan Creek (see Figures 1 and 2 in Karr and others 1987). Similarly, Steedman (1988) also observed considerable natural variation in stream fish communities and IBI, with most of the variation being due to annual rather than seasonal components of variability.

These results suggest long-term monitoring of stream fishes is critically needed throughout drainage basins to establish the natural range of temporal variation in community structure. Such research is necessary so that techniques for segregating natural from anthropogenically induced variation can be developed and will be roughly analogous to defining criteria and standards for specific pollutants (Karr and others 1986). Once achieved, it will allow regulatory agencies to distinguish anthropogenic from natural disturbance with greater reliability and will prevent the expenditure of time and money trying to "fix" temporal changes in fish communities that were due to natural environmental fluctuations.

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