The Decline of the Blue Crab

Changing weather patterns and a suffocating parasite may have reduced the numbers of this species along the Eastern seaboard

Richard F. Lee and Marc E. Frischer

Most of us encounter the blue crab, *Callinectes sapidus,* on a dinner plate—often in an unrecognizable mass described as a "crab cake." The blue crab's participation in various appetizing recipes supports an important fishery along the Atlantic and Gulf coasts of the United States, where tens of millions of crabs are harvested annually. In recent years, however, the commercial crab industry on the East Coast has suffered a significant decline. Blue crab landings along coastal Georgia, for example, dropped well below the 45-year average of 3.9 million kilograms to about 816,000 kilos in 2002. The effect of this dramatic crash has been catastrophic. Fishermen whose families have caught blue crabs for generations are going bankrupt, and the cost of crabs for consumers has soared.

The ecological and economic impacts have motivated several investigations into the cause of the decline. There are hints that weather-related changes may be responsible. There is also evidence that a parasitic disease in blue crabs has become both more prevalent and more severe. Our group has been studying these events along the coast of southeastern Georgia, a region that has been hit especially hard, to see whether the two phenomena might be related. These investigations are helping us to understand the conditions that led to the outbreak of disease in the blue crab population.

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A Consuming Pathogen

Blue crabs on the East Coast appear to be suffering from a parasitic infection of a dinoflagellate called *Hematodinium perezi*. This parasite was first reported back in 1931 from crabs collected along the French coast. *Hematodinium* is related to two other toxic dinoflagellates: *Gymnodinium brevis,* which causes the red-tide algal blooms, and the fish-killing *Phiesteria piscicida*. In the past few decades, outbreaks of *Hematodinium* have reduced populations in a number of commercially important crab fisheries throughout the globe, including Alaska, Newfoundland, Scotland and France.

Hematodinium is a noxious pathogen that proliferates in the crab's blood, the hemolymph. As it grows inside the crab, the parasite consumes the hemolymph cells and the primary hemolymph protein, hemocyanin. This protein transports oxygen in crustaceans in much the same way that hemoglobin performs this task in vertebrates. Crabs suffering from a heavy infection of *Hematodinium* are lethargic and eventually die from suffocation for lack of oxygen.

The blue crab appears to be particularly susceptible to infection by this dinoflagellate. Part of the reason may be the defense mechanisms that blue crabs use to protect themselves against infections. Crustaceans lack the specialized immune system of vertebrates and instead depend on nonspecific blood cells called *hemocytes.* These cells encapsulate parasites in nodules, which are then processed for elimination. This mechanism seems to be most effective in cold conditions when parasites such as *Hematodinium* are less metabolically active, and, indeed, winter crabs are generally free of the dinoflagellate. However, during a heavy infection, the hemocytes are overwhelmed by the prolific reproduction of the parasite, and the crab succumbs to the disease. The apparent inadequacy of the blue crab's defense mechanism isn't the complete story, however. Other crabs, including the closely related lesser blue crab *(Callinectes similis),* do not appear to be susceptible to *Hematodinium* infection at all. So there must be something unique about the interaction between *Hematodinium* and the blue crab.

In this light, we have been investigating the life cycle of *Hematodinium*, which takes place largely inside the blue crab. The parasite has several distinct life stages, including a trophont form, a mobile vegetative plasmodium, a dinospore and a prespore, called a *merozoite.* It appears that the vegetative plasmodium can become a plasmodium mother cell, or *schizont.* The schizont then produces daughter cells, the merozoites, which later develop into dinospores.

The details of this life-history model are still speculative because it is very difficult to culture *Hematodinium.* Recently, however, we were able to observe a metamorphosis of the trophont stage, the most common form observed in crab hemolymph, into a small flagellated type that appears to be a dinospore. The mobile dinospore is believed to be

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Figure 1. Blue crab *(Callinectes sapidus)*, which is harvested by the millions every year, supports an important fishery along the Eastern and Gulf coasts of the United States. However, a recent crash in the blue crab population has devastated the commercial crab industry. The authors investigate the cause of the decline in southeastern Georgia by examing the relation between crabs infected with a parasitic dinoflagellate and a prolonged drought.

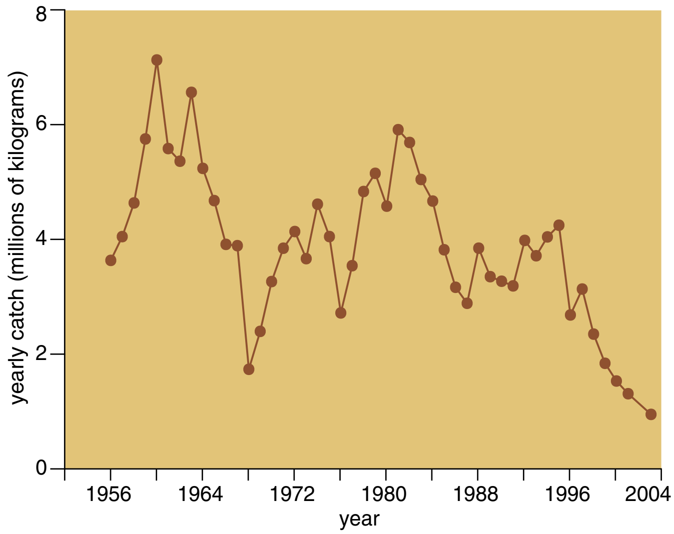

Figure 2. Yearly catch of blue crabs in coastal Georgia since 1954 reveals a sharp plunge in the past few years, culminating in a new low in 2003 *(left)*. A Georgia crabber in Sapelo Sound *(right)* hauls in a modest catch, which typically includes some infected crabs. (Data obtained from the Georgia Department of Natural Resources in Brunswick, Georgia.)

involved in the transmission of the disease in the environment, possibly forming a sporocyst once it is in the water.

Diagnosing *Hematodinium* disease depends on detecting the parasite in blood samples. When the pathogen is present in relatively high concentrations—say, more than 1 parasite per 300 normal blood cells—*Hematodinium* can be detected in the light microscope by using special stains. However, these techniques are of little use for detecting the organism when it is present in low concentration or when it is outside the crab host.

Our research group recently developed a gene-based diagnostic test for *Hematodinium* that is capable of detecting the organism at concentrations as low as 1 parasite per 300,000 normal blood cells. The technique can also be used to identify the organism outside the crab. Equipped with these new diagnostic tools, we have been studying the life cycle and the distribution of *Hematodinium*, as well as the disease outbreaks among blue crabs.

The transmission of the disease between crabs is central to understanding its epidemiology. The dinospore is thought to play a crucial role. It is generally believed that the dinospore leaves the crab via the gills, enters the surrounding water and remains infectious in a resting stage. Our fieldwork and laboratory investigations support this view. We have detected *Hematodinium* in the waters of Wassaw Sound, Georgia, during the peaks of several disease outbreaks, suggesting that the parasite is indeed released into the water from infected crabs. Moreover, healthy, disease-free crabs exposed to this water can become infected. Laboratory studies show that *Hematodinium* can be released into the water by sick crabs. No one knows how long the parasite can persist in the water, but we were able to detect the organism three weeks after an infected crab had died and been removed from a tank.

Although *Hematodinium* can be transmitted through the water, the rapid spread of the disease during an epizootic is probably due to cannibalism. Blue crabs are notoriously cannibalistic, and as soon as one is weakened by disease it quickly falls prey to its neighbors. In laboratory studies healthy crabs that are fed tissue from infected crabs almost invariably contract the disease.

Weather and Disease

If *Hematodinium* disease is indeed the cause of the great decline in blue crab numbers, we need to determine why the parasite has suddenly become so deadly. A strategy of our investigations has been to compare the prevalence and intensity of *Hematodinium* disease in blue crabs found in two adjacent estuary systems on the Georgia coastline: Wassaw Sound and Ossabaw Sound. Although these systems are located within 20 kilometers of each other, they have different salinity profiles. Ossabaw Sound and its associated freshwater rivers are characterized by areas of low salinity. Following a heavy rain, which dramatically increases freshwater input into the sound from the Ogeechee River, salinities in Ossabaw Sound creeks can be as low as 1 part per thousand. In contrast, the salinity of creeks that feed Wassaw Sound are typically around 25 to 30 parts per thousand. By comparison, the average salinity of seawater is approximately 35 parts per thousand. A prolonged drought, from 1997 to 2002, resulted in higher than normal salinities in both sounds.

Standard histological techniques indicate that crabs caught during the winter are free of infection. However, the prevalence and intensity of the disease increases in late spring through early summer, and this is associated with the disappearance of the crabs in the summer. The crabs and the disease tend to reappear in the fall.

The more sensitive gene-based diagnostic technique revealed that *Hematodinium* was present at very low levels in a few crabs during the winter, indicating that the disease had not disappeared completely. An interesting exception to this pattern was observed in 2001–2002, when moderately infected crabs were found throughout the winter. Considerably higher than average temperatures persisted during the winter of 2001–2002, suggesting that the warmer weather contributed to the maintenance of the disease in winter crabs.

Despite the absence of crabs in most of Wassaw Sound during the summers, we did find crabs from a creek that was fed with freshwater from an underground spring. The salinity (24 parts per thousand) and temperature (22 degrees Celsius) in the bottom waters of this creek were considerably lower than the average conditions (34–35 parts per thousand and 30 degrees) in Wassaw Sound during this period.

The presence of *Hematodinium* disease during a warm winter and the presence of healthy crabs during summer in a cool, low-salt creek indicate that both temperature and salinity are primary variables controlling the prevalence and intensity of the disease.

In contrast to the low catches and high disease prevalence in Wassaw Sound and its associated estuarine rivers, the Wilmington and the Skidaway, infected crabs were rarely observed in Ossabaw Sound between 1998 and 2001. And infected crabs were never seen in an associated freshwater river, the Ogeechee. However, in the fall of 2001, *Hematodinium*-infected crabs became more common in Ossabaw Sound, and crab landings dropped. Despite the emergence of *Hematodinium* disease in Ossabaw Sound in the fall of 2001, crabs collected from the Ogeechee River remained free of the disease.

Because the water temperatures in the Ossabaw and Wassaw sounds are similar, these observations suggest that *Hematodinium* disease outbreaks are more likely when the flow of fresh water to estuarine systems is reduced and the salinity is high—greater than 28 parts per thousand.

On the other hand, a 20-year record

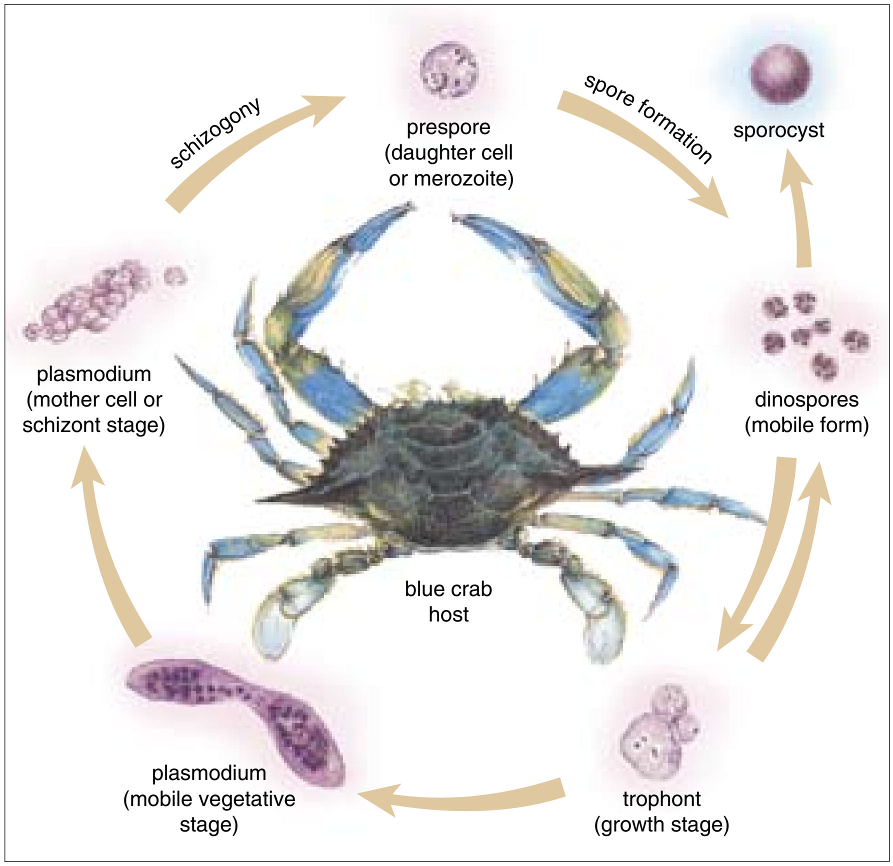

Figure 3. Parasitic dinoflagellate *Hematodinium* lives much of its life cycle inside the blue crab, and is generally believed to be the cause of the crab's recent decline. The blue crab's susceptibility to *Hematodinium* is unexplained—a closely related crab species appears to be unaffected by the disease. Unfortunately, solving the mystery is proving to be tricky because it is difficult to culture the dinoflagellate's life stages in the laboratory. The mobile dinospore is thought to be an infectious stage that can survive in water for long periods, possibly encapsulated in a sporocyst. However, the blue crab may also acquire the disease by eating infected amphipods or other infected crabs. Spider crabs, stone crabs and mud crabs also have a high mortality when infected with *Hematodinium*.

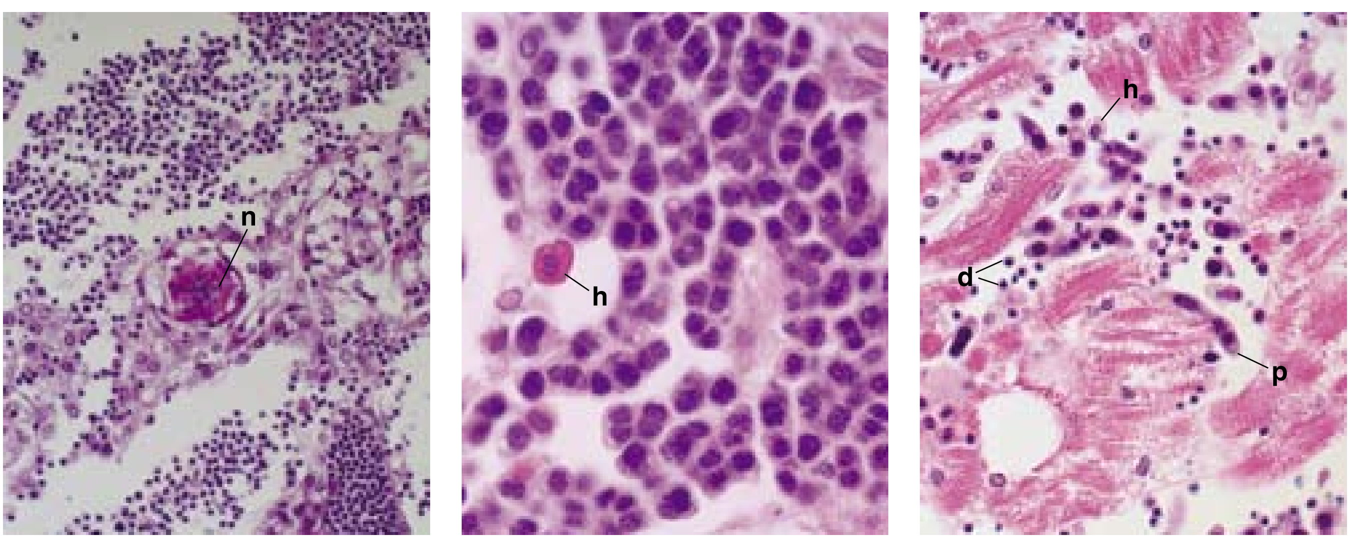

Figure 4. *Hematodinium* cells *(purple)* infiltrate various tissues in the blue crab. The blue crab's only known defense against the dinoflagellate is to surround the invader with protective hemocytes *(left)*, which can contain the parasite inside a nodule *(n)*. Unfortunately, this defense mechanism can be easily overwhelmed by the sheer number of parasites, as seen in the vascular space *(middle)* of a heavily infected crab, which is packed with trophonts *(purple)* and a lone hemocyte *(h)*. Similarly, the cardiac muscle of an infected crab *(right)* is crowded with plasmodial forms *(p)* and dinospores *(d)*, which easily outnumber the host's hemocytes *(h)*. (Images courtesy of Anna Walker, Department of Pathology, Mercer University School of Medicine.)

Figure 5. Assay for *Hematodinium* using a gene-based technique is a thousand times more sensitive than a standard analysis using the light microscope. *Hematodinium* is revealed by the presence of a 196-base-pair fragment of the parasite's genomic DNA in samples drawn from the blood of lightly infected blue crabs *(lanes 8 and 9)* and a moderately infected blue crab *(lane 10)*. Healthy crabs *(lanes 4, 5, 6 and 7)* lack this fragment. The results are compared to a molecular-weight "ladder" consisting of 100-base-pair "rungs" *(lane 1)*, a blank negative control *(lane 2)* and a positive control *(lane 3)*. The method allows scientists to detect free-living *Hematodinium* in the water and at extremely low levels in otherwise healthy crabs. This figure simulates the results of an agarose gel assay.

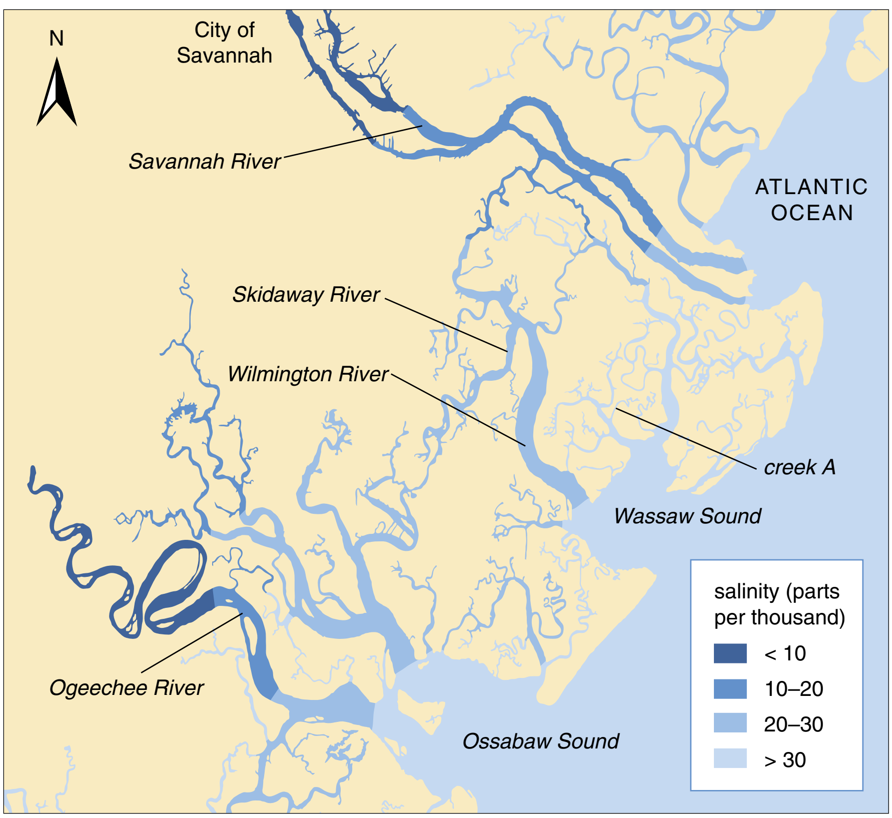

Figure 6. Different salinity profiles distinguish the Wassaw and Ossabaw Sounds along the coast of Georgia. Wassaw Sound and its estuarine rivers, the Wilmington and the Skidaway, tend to have relatively high salinities compared with Ossabaw Sound and the freshwater Ogeechee River that feeds it. The higher salinities of the Wassaw Sound are associated with an increased prevalence of *Hematodinium* disease and fewer crabs compared to Ossabaw Sound. However, a small tributary *(creek A)* in the Wassaw Sound region was apparently fed by an underground spring and maintained a healthy crab population. All of these observations suggest that a recent drought, which increased the salinities of both sounds, was responsible for the high incidence of *Hematodinium* disease and the decline of the blue crab population.

of blue crab catches in the Georgia fishery suggests that the inverse is also true: Lower salinity in estuaries seems to be associated with increases in the blue crab population. Between 1970 and 1990, large catches were positively correlated with a high river flow, suggesting that the availability of fresh water was beneficial to the health of the crab population. Rain in coastal Georgia has increased to normal levels during the past nine months, and the drought has officially ended. Although crab populations did not increase in 2003, commercial and recreational fisherman anecdotally report catching more crabs in 2004. We have likewise observed a decline in the prevalence and intensity of *Hematodinium* disease. Although it is still too early to determine whether crab numbers will return to their pre-drought levels, these observations further support the link between rainfall, disease and the blue crab population.

A large survey of crabs collected by Gretchen Messick of the National Oceanographic and Atmospheric Administration Laboratory in Oxford, Maryland, and Jeffrey Shields from the Virginia Institute of Marine Sciences, also indicates that the outbreaks of the parasitic disease are related to water salinity. From the Chesapeake Bay to Florida on the Atlantic coast, and from Florida to Texas along the Gulf of Mexico, Messick and Shields found that *Hematodinium* was absent in blue crabs when the salinity was less than 11 parts per thousand, or when the average winter temperatures of the water were below 10 degrees Celsius.

All of these observations are consistent with the hypothesis that lower salinity reduces the mortality of *Hematodinium*-like protozoan diseases. Why might this be so? One possibility is that free-living dinospores do poorly in low-salinity waters. Certainly, in our laboratory studies *Hematodinium* did not survive well in a low-salt culture medium. Another possibility is that blue crabs are better able to resist infection by *Hematodinium* in low-salt conditions, but the mechanism for this is not clear.

The Cause of the Decline

A second focus of our investigations has been to determine whether the increase in *Hematodinium* disease is sufficient to have caused the decline of the blue crab. We addressed this question with a series of observations and experiments.

First we had to demonstrate that the disease was, in fact, deadly to blue crabs. In one simple experiment, we found that heavily infected crabs that were maintained in parasite-free water typically died within 48 hours. In a follow-up study, 10 *Hematodinium*-free crabs, originally caught from the Ogeechee River, were transferred to Wassaw Sound during a peak infection period. After 72 hours, 4 of the crabs had become infected with *Hematodinium* and died. In another instance, there was a report of several hundred dead crabs washing ashore near Brunswick, Georgia, where *Hematodinium* had been detected. All of the dead crabs we examined there were infected with the parasite.

These studies and field observations all point to *Hematodinium* as the cause of the dramatic reduction in the blue crab population in Wassaw Sound. By extension, it seems likely that this parasite at least contributed to, if not caused, the overall decline of the blue crab in the southeastern United States.

The devastation of a marine species by a disease has been reported before, but this is the first time that a highly mobile marine species has been cut down by disease. Correlations between protozoan-caused diseases and climatic changes have been described in a number of sessile estuarine species. Well-documented examples include the protozoan parasites *Haplosporidium nelsoni* and *Perkinsus marinus*. These pathogens cause diseases called MSX and Dermo, which have devastated the eastern oyster, *Crassostrea virginica,* along the Atlantic and Gulf coasts of the United States. Because these parasites cannot survive in low-salinity waters, the prevalence of these diseases is inversely related to rainfall and freshwater discharge into estuarine system. This is similar to our observations of *Hematodinium* disease in blue crabs.

Stormy Weather?

Surprisingly, the relation between disease, weather and the health of a fishery has rarely been considered. However, the aggravation of a disease in a marine species by a regional change in weather may be a harbinger of the future if global changes in climate continue. Such impacts are becoming indisputable as scientists repeatedly observe effects on the distributions of plant and animal populations in tandem with changes in weather patterns, global temperatures and the composition of the atmosphere. Unfortunately, the outcomes of such changes are not always easy to predict because they depend on indirect interactions between complex organisms.

Furthermore, the consequences of disease may be more profound than one might predict from simple increases in mortality. For example, it may be that *Hematodinium* preferentially kills female blue crabs. Since female crabs must traverse high-salinity estuarine areas to reach offshore spawning grounds, they are more likely to contract the disease than males, which can remain in areas of lower salinity year round, and so avoid infection. As a result, *Hematodinium* disease may be affecting the reproductive success of crab populations at the same time that it skews the sex ratios and reduces standing stocks. This possibility remains unexplored.

What the future holds in store remains unknown. The lesson we take away from these studies is that a prolonged change in the weather may have dramatic effects on marine life by altering the delicate balance between an organism and a pathogen.

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