Predation of freshwater fish in environments with elevated carbon dioxide

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Abstract. Carbon dioxide (CO\textsubscript{2}) in fresh-water environments is poorly understood, yet in marine environments CO\textsubscript{2} can affect fish behaviour, including predator–prey relationships. To examine changes in predator success in elevated CO\textsubscript{2}, we experimented with predatory \textit{Micropterus salmoides} and \textit{Pimephales promelas} prey. We used a two-factor fully crossed experimental design; one factor was 4-day (acclimation) CO\textsubscript{2} concentration and the second factor CO\textsubscript{2} concentration during 20-min predation experiments. Both factors had three treatment levels, including ambient partial pressure of CO\textsubscript{2} (pCO\textsubscript{2}; 0–1000 \textmu atm), low pCO\textsubscript{2} (4000–5000 \textmu atm) and high pCO\textsubscript{2} (8000–10000 \textmu atm). \textit{Micropterus salmoides} was exposed to both factors, whereas \textit{P. promelas} was not exposed to the acclimation factor. In total, 83 of the 96 \textit{P. promelas} were consumed (n = 96 trials) and we saw no discernible effect of CO\textsubscript{2} on predator success or time to predation. Failed strikes and time between failed strikes were too infrequent to model. Compared with marine systems, our findings are unique in that we not only saw no changes in prey capture success with increasing CO\textsubscript{2}, but we also used CO\textsubscript{2} treatments that were substantially higher than those in past experiments. Our work demonstrated a pronounced resiliency of freshwater predators to elevated CO\textsubscript{2} exposure, and a starting point for future work in this area.


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Introduction

The effects of carbon dioxide (CO\textsubscript{2}) on aquatic systems has recently received a great deal of interest (Fabry et al. 2008; Munday et al. 2008). Many of the questions on this topic, and much of the work, is motivated by increasing concentrations of CO\textsubscript{2} in the atmosphere and the commensurate increase of CO\textsubscript{2} concentrations in aquatic environments (often measured as the partial pressure of CO\textsubscript{2} (pCO\textsubscript{2}; Solomon et al. 2007). Marine systems have been particularly responsive to concerns over elevated pCO\textsubscript{2}, given the nature of ocean acidification; elevations in atmospheric CO\textsubscript{2} translate into an increase in the pCO\textsubscript{2} in the oceans, which, in turn, causes acidification that can negatively affect a range of biological processes, including fish behaviour (Caldeira and Wickett 2003). Fewer studies have been undertaken to understand and quantify how the concentration of fresh-water CO\textsubscript{2} may change in the future (but see Butman and Raymond 2011; Hasler et al. 2016a). However, currently evidence is mounting to support the idea that pCO\textsubscript{2} in North American fresh waters may be higher and more variable than conventionally assumed (Maberly 1996; Phillips et al. 2015), and freshwater biota may be at risk from increasing pCO\textsubscript{2} (Hasler et al. 2016a).

In North American fresh waters, pCO\textsubscript{2} is demonstrating to be dynamic and variable. Cole et al. (1994) found that the majority of sampled US lakes are supersaturated with pCO\textsubscript{2}, whereas Butman and Raymond (2011) showed that many streams across the US are supersaturated with pCO\textsubscript{2}. Furthermore, Baumann et al. (2015) reported CO\textsubscript{2} dynamics in brackish systems and found additional evidence for high variability in pCO\textsubscript{2}; e.g. daily summer values ranged from 500 to 4000 \textmu atm. Concentrations of pCO\textsubscript{2} can be particularly high and variable in low-order streams in watersheds, with high terrestrial primary productivity and precipitation rates (Butman and Raymond 2011), and in watersheds underlain with geology that does not allow for pH buffering (Cole et al. 1994). In addition to interest in the overall magnitude of CO\textsubscript{2}, there is high variability of pCO\textsubscript{2} in fresh waters. This high variability is largely absent from CO\textsubscript{2} investigations in the marine realm, at least with respect to coral-reef environments that have been investigated (Munday et al. 2014). In addition to natural sources, proposed deployments of fish
barriers that use CO2 (Noatch and Suski 2012) represent another potential source of significant (but localised) CO2 input to fresh waters.

Predator–prey dynamics can be among the most important interactions in which fish participate. Successful predation is not only needed for survival, but effective predation can lead to variation in growth, maturation and other life-history traits that shape individual selection, population growth and evolution (Lima 1998). The same can be said for avoiding predation; those individuals best equipped to avoid predation will have higher fitness within their population. Because predator–prey dynamics are critically important for both species involved, but also for the structuring of the food web and ecosystem, minor changes in this dynamic can have substantial effects (Kitchell et al. 1994). Water-quality parameters are known to affect predator success and prey avoidance (e.g. turbidity; Rahel and Nutzman 1994); however, very little work has looked at how increases in pCO2 may alter this interspecies dynamic, with studies thus far having been limited to marine environments. Ferrari et al. (2011) examined predation with Pseudochromis fuscus preying on Pomacentrus spp. in control (440 μatm) and elevated (700 μatm) CO2 environments, and found that predation rates increased with elevated pCO2, but that there was no change in prey selectivity on smaller prey (and a reversal of prey species at larger sizes). Allan et al. (2013) also experimented with reef-fish predation under control (440 μatm) and elevated (880 μatm) pCO2 conditions. In a cross-factorised design, Pseudochromis fuscus and prey Pomacentrus amboinensis were exposed to either treatment, with results suggesting negative effects for both species in elevated pCO2; predators showed reduced capture success and prey showed longer reaction distances. Thus, exposure to elevated pCO2 can induce changes to the predator–prey dynamics of marine fishes, which, in turn, can translate into population-level changes (Munday et al. 2010).

In the current study, we sought to expand on previous work in the marine environment by quantifying how CO2 exposure would affect predator–prey dynamics for freshwater fishes, as well as the interaction of CO2 concentrations, along with the duration of exposure. More specifically, the objective of the present study was to quantify predator–prey outcomes in fishes in an experimental setting, following exposure to various levels of pCO2. Micropterus salmoides was used as a predator species and Pimephales promelas was used as a prey species. Understanding the influence of CO2 on predator–prey dynamics in fresh water will help understand how species and communities exposed to increasing concentrations of CO2 can expect to respond. We predicted that predation rates, successful consumption, time to consumption, and failed strikes would be affected by increasing pCO2. Particularly, we expected that time to consumption and failed strikes would increase with pCO2, and overall predation success (capture of prey after a fixed amount of time) would decrease.

**Materials and methods**

**Species and acclimation**

We used Micropterus salmoides as a predator species and Pimephales promelas as a prey species. Both of these fish species are common in North American fresh waters and have a well-documented predator–prey relationship (Hambright 1991). All fish were captive-reared and acquired from Keystone Hatcheries in Richmond, Illinois, USA, in early November 2015. Fish were transported to and held at the Aquatic Research Facility at the University of Illinois Urbana–Champaign. On arrival to the facility, conspecifics were held in three 1100-L aquaria (no more than 40 M. salmoides individuals per aquarium) with ambient pCO2 (<1000 μatm) and a constant temperature of 24°C (range 23.8–24.7°C). Pimephales promelas was initially introduced to the M. salmoides-holding tank to confirm a predation response (which was unknown because of hatchery diet), and, almost instantly, M. salmoides aggressively pursued prey. After this confirmation of predation response, M. salmoides were left for 1 week without food, to ensure that all predators were sufficiently hungry during the experiments. Ammonia and nitrate concentrations were monitored (LaMotte Co., Ammonia Nitrogen kit number 3351-02, Chestertown, MD, USA) and daily water changes took place. To prevent hypoxia, air was bubbled in and dissolved oxygen monitored (YSI, 550A Yellow Springs 82 Instruments, Irvine, CA, USA).

**Experimental setup**

The experimental design included a 3 × 3 factorial design, in which the two factors were pCO2 during holding (4-day acclimation) and pCO2 during the experiment (20 min). These factors were selected to compare the effects of longer-term, pre-predation conditions with those at the time of predation. Micropterus salmoides individuals were exposed to both factors, whereas P. promelas individuals were all acclimated to ambient pCO2 and exposed to higher pCO2 only during the experimental phase. Each factor had the following three levels with a target concentration: ambient pCO2 (0–1000 μatm), low pCO2 (4000–5000 μatm) and high pCO2 (8000–10 000 μatm). These levels were chosen such that the control represented normal conditions, 4000–5000 μatm represented higher than normal conditions, (but values that are not considered extreme in fresh water) and 8000–10 000 μatm was selected as an upper limit of pCO2 tolerance. Previous work has shown that extended holding at pCO2 > 10 000 μatm can have strong negative effects on fish, such that they lose equilibrium (Kates et al. 2012). Experimental pCO2 values were maintained using the common method of bubbling CO2 gas into the water through an airstone, using water pH to maintain a target pCO2 level (Pinpoint pH controller, American Marine Inc., Ridgefield, CT, USA; Kates et al. 2012; Hasler et al. 2016b). This was performed in a header tank, from which treated water was then mixed into the experimental tanks. A modified infrared CO2 probe was used to monitor pCO2 (GMT221, 0–20%, Vaisala, Vantaa, Finland; Johnson et al. 2010). Temperature and CO2 measurements for all trials (n = 96) are reported in Table 1. The pCO2 monitoring was accurate to ± (1.5% of range + 2% of reading) (Vaisala), and probe values were also compared with water with known concentrations of pCO2 multiple times throughout the study period.

After the 20-min acclimation phase for the predator, one prey fish was introduced to the aquaria holding nothing but the predator fish. Aquaria contained no shelter and low light (aquaria were in a lighted room, but behind black curtains on all sides to minimise visual distraction), suggesting that visual
cues were the primary means of predation. All trials were recorded from an overhead camera. We watched videos of all trials, and determined whether the prey was consumed (yes or no), the time to consumption (s), the number of total strikes, the number of failed strikes, and the time between multiple strikes (s). Water temperature was constant (varying less than \(1^\circ C\) throughout the experiment) and was not included in the analysis, and \(pCO_2\) concentrations were treated as factors because their measurements did not vary meaningfully within factor level. Although prey size can be viewed as a factor and some studies seek to quantify this, we selected sufficiently large predators and small prey, so that fish sizes were not considered an important influence on predation (Goldstein 1993). For example, mean predator size was 180 mm (\(n = 24\); s.d. = 14) and prey size was 51 mm (\(n = 24\); s.d. = 5). Such a large size differential and strong support in the literature suggests that size and gape limitation were not a factor in our experiments.

### Data analysis

We focused on two statistical models to describe predation at varying levels of \(pCO_2\). The first model was selected to answer the question of whether \(CO_2\) treatments affected successful consumption of \(P.\) promelas. The model used to address this question was a binomial generalised linear model (i.e. logistic regression) that used the categorical predictors of acclimation \(pCO_2\), experimental \(pCO_2\), and their interaction, to predict the probability of whether or not \(P.\) promelas was consumed.

The second question we sought to answer was whether \(CO_2\) treatments affected the time it took a \(M.\) salmoides individual to successfully consume a \(P.\) promelas individual. The model used to address this question was a beta regression, which is commonly used to model rates and proportions (Ferrari and Cribari-Neto 2004). In our case, time to consume was bounded at 0 and 1200 s, and the individual trial times were divided by the total time (1200), resulting in the proportion used as the response variable. Again, we used the categorical predictors of acclimation \(pCO_2\), experimental \(pCO_2\), and their interaction, to model the time it took for \(P.\) promelas to be consumed.

### Results

Overall, 83 of the 96 \(P.\) promelas individuals were consumed during the 96 trials. For both the logistic- and beta-regression
models, we first ran an interaction-only model to test for an interaction between the main effects of acclimation \( p \text{CO}_2 \) and experimental \( p \text{CO}_2 \), the presence of which would exclude the need to examine main effects. The interaction-only logistic regression (which modelled predation success) showed significant differences between some groups (i.e. 95% credible intervals of differences between group means did not overlap with zero; Fig. 1), which eliminated the need to run a main-effects model. The treatment combinations showed significant differences, with the acclimation control/\( \text{CO}_2 \) experimental high \( p \text{CO}_2 \) having the lowest proportion of prey-consumption success (mean = 0.64 and 95% credible interval = 0.29–0.90), and the acclimation control/\( \text{CO}_2 \) experimental low \( p \text{CO}_2 \) and acclimation high/\( \text{CO}_2 \) experimental high \( p \text{CO}_2 \) having very high estimated prey-consumption success (both with a mean = 1.0 and 95% credible interval = 0.95–1.00).

The interaction-only beta-regression model (which modelled the time to prey consumption) found no significant differences across treatments (Fig. 2), and, subsequently, main effects were examined. We used separate one-way main-effect models for each factor, because means parameterisations were needed to generate full posterior estimates for all effects required for multiple comparisons (i.e. effects parameterisations require setting one factor level to 0, which eliminates the posterior distribution needed for multiple comparisons). Additionally, means parameterisation of two-way models results in model non-identifiability. The single-factor beta-regression model for acclimation \( \text{CO}_2 \) concentration to predict time until prey consumed. Time until consumption decreased with an increasing \( \text{CO}_2 \) concentration, although all factor levels overlapped at the 95% credible level.

Owing to the very few trials with failed strikes (only 4 of 96), we did not model failed strikes or time between failed strikes, nor were these few observations of failed strikes occurring within one treatment type. Finally, a logistic regression model was fitted to test for an effect of experimental day on predation success, so as to determine whether predators were more or less likely to successfully consume as the experiment progressed (i.e. examining the potential effect of hunger). Experimental day showed no significant effect, indicating that holding time did not influence a predator’s probability of consuming prey.

Fig. 1. Estimates of interaction coefficients for an interactions-only logistic-regression model. The x-axis lists the interaction combinations, with letters A and E indicating Acclimation (4-day holding) and Experimentation (20-min trial) treatments respectively, and subscripts C, L, and H indicating \( \text{CO}_2 \) treatment levels control, low and high respectively. Within the plotting surface, letters A and B are groupings for multiple comparisons; groups sharing the same letter are not significantly different at the 95% credible level.

Fig. 2. Estimates of interaction coefficients for an interactions-only beta regression model. The x-axis lists the interaction combinations, with letters A and E indicating Acclimation and Experimentation treatments respectively, and subscripts C, L, and H indicating \( \text{CO}_2 \) treatment levels control, low and high respectively. No significant differences among groups were found at the 95% credible level.

Fig. 3. Coefficient estimates from a one-way beta regression using acclimation \( \text{CO}_2 \) concentration to predict time until prey consumed. Time until consumption decreased with an increasing \( \text{CO}_2 \) concentration, although all factor levels overlapped at the 95% credible level.
that P. fuscus found that P. fuscus consumption decreased with an increasing CO2 concentration, although all addition to studies on Clements and Hunt 2015). Specifically, Allan observed, including several shark species, which avoided prey high prey consumption rate and time to prey consumption. In fact, might alter pursuit, capture and ingestion of prey is unknown, Comparison to marine studies Coefficient estimates from a one-way beta regression using experimental CO2 concentration to predict time until prey consumed. Time until consumption decreased with an increasing CO2 concentration, although all factor levels overlapped at the 95% credible level.

Discussion

Comparison to marine studies

Acclimation to elevated pCO2 for 4 days did not result in alterations to feeding behaviours for M. salmoides, defined as prey consumption rate and time to prey consumption. In fact, M. salmoides acclimated to both low (4000–5000 µatm) and high pCO2 (8000–10 000 µatm) consumed 86% of prey items. These findings contradicted recent experiments with marine fishes that found that predator–prey dynamics were compromised when fish were exposed to elevated pCO2 (441–1064 µatm, which is ∼1.1–2.5 times ambient pCO2; reviewed by Clements and Hunt 2015). Specifically, Allan et al. (2013) found that P. fuscus had a lower capture success when both P. fuscus and its prey items were exposed to elevated pCO2 (880 µatm, or 2.0× ambient pCO2) for 4 days. In another study, Cripps et al. (2011) found that olfactory response of P. fuscus to the smell of injured prey was degraded, fish took more than four times longer to respond to introduced prey, and fish had almost one-third fewer feeding strikes when exposed to elevated pCO2 (600–950 µatm, or 1.5–2.4× ambient pCO2) for 4–7 days. In addition to studies on P. fuscus, effects of CO2 on the predator mechanics of other obligate marine fish predators have also been observed, including several shark species, which avoided prey odours after exposure to elevated pCO2 (Green and Jutfelt 2014; Dixon et al. 2015; Pisteves et al. 2015). Of particular note is that pCO2 in fresh waters tends to be in much higher concentrations, which is why our values are substantially greater than those presented in the (marine) literature.

Possible mechanisms

Mechanistically, the successful ingestion of a prey item requires the coordination of a number sensory modalities, including chemical and visual detection of a prey item, followed by pursuit, capture and ingestion (Clements and Raubenheimer 2006; Allan et al. 2013). Precisely how exposure to elevated pCO2 might alter pursuit, capture and ingestion of prey is unknown, but the influence of environmental variability on fish performance is of interest to researchers (Claireaux and Lefrançois 2007). Currently, it is believed that exposure to elevated pCO2 negatively affects prey detection of predators, leading to reductions in feeding rates (Cripps et al. 2011). More specifically, as a result of CO2-induced acidosis in the blood of fish, there is an increase in extracellular Cl– concentrations (Heuer and Grosell 2014), which causes increased neuronal depolarisation and altered function of the GABA_A neurotransmitter receptor (Nilsson et al. 2012). This alteration in the receptor is thought to be responsible for a wide array of behavioural and physiological changes in fishes and could be responsible for altered prey detection (Nilsson et al. 2012; Hamilton et al. 2013; Chivers et al. 2014; Clements and Hunt 2015; Ou et al. 2015). Changes in pCO2 can alter the GABA_A neural transmitter in obligate freshwater fishes (Regan et al. 2016); however, without a defined link between prey capture and exposure to elevated pCO2, it is difficult to assess whether M. salmoides in the present study experienced a compromised GABA_A pathway. Despite the lack of defined physiological links, it is clear that the ability of M. salmoides to capture and consume prey was not altered despite exposure to elevated pCO2.

Similarly to feeding after extended exposure to elevated pCO2, feeding behaviours of M. salmoides were not affected by short-term holding at elevated pCO2. Fish acclimated to ambient pCO2 and then placed in either low or high pCO2 tanks 20 min before the feeding trial did not show a significant change in either prey consumption rates or in the time to consume prey. Behaviour after short-term exposure to elevated pCO2 is important to understand because freshwater pCO2 can vary over both diel and seasonal time scales (Maberly 1996). For example, as a result of factors that include rain events, season and aquatic respiration, pCO2 can rise in freshwater lakes within a day (100-fold change in some days; Maberly 1996). In addition, zones of elevated pCO2 that are ∼50-fold above the ambient concentration have been proposed for use as a non-physical barrier to influence the movement of fishes (Kates et al. 2012; Noatch and Suski 2012). Thus, wild, free-swimming fish have potential to experience sudden increases in pCO2 independent of insidious stressors such as climate change. Should short-term increases in pCO2 be high enough (e.g. >45 000 µatm), fish may lose equilibrium, because CO2 is a known anaesthetic for fish (Marking and Meyer 1985). Also, mortality may be possible because cardiac failure occurs when marine fishes have been exposed to elevated pCO2 (~50 000 µatm; Ishimatsu et al. 2004). However, in natural environments, where a gradient in CO2 concentrations exist, fish have the capacity to sense elevated pCO2 (Perry and Gilmour 2002) and will avoid lethal concentrations (Kates et al. 2012). Despite fish having the ability to avoid elevated pCO2, short-term physiological consequences are possible, because physiological changes in response to CO2 exposure are rather quick (e.g. changes occur within minutes (Iwama et al. 1989; Ishimatsu et al. 2004). In addition, the rate at which the GABA transmitter pathway is altered and causes behavioural changes can occur within 4 days (Ishimatsu et al. 2004; Nilsson et al. 2012), but physiological effects are possible within hours (Chivers et al. 2014). So, it is conceivable that short-term exposure to elevated pCO2 had the potential to influence the feeding behaviours of M. salmoides;
however, clearly, data from the current study showed that short-duration exposures to high concentrations of CO2 do not affect consumption rates or time to consumption.

There are several potential mechanisms to explain why exposure to elevated pCO2 did not alter the feeding behaviours of M. salmoides. First, and perhaps foremost, the range of pCO2 values that freshwater fish have been exposed to over evolutionary history is likely to be greater than that of marine fishes. Specifically, pCO2 in freshwater lakes can range from ~100 to 4100 µatm and can reach as high as 20 000 µatm in some African lakes (Cole et al. 1994). In comparison, marine environments are typically at equilibrium with atmospheric pCO2 (~400 µatm with very little variability in most marine habitats) and are expected to reach 1000 µatm by 2100 (Solomon et al. 2007); however, CO2 ‘hotspots’ where pCO2 can be 10-fold above the current level exist, and can be found in the Southern Ocean, Pacific Ocean and North Atlantic Ocean (McNeil and Sasse 2016). Similarly, pCO2 levels in coral reefs, where several studies have observed changes to predator–prey dynamics, are typically stable and close to the mean ocean pCO2 (Munday et al. 2014). For this reason, freshwater fish may be adapted to a wider range of pCO2 values, as well as higher absolute pCO2, and thus may have the ability to maintain typical feeding behaviours following holding at an elevated pCO2. For example, cobia (Rachycentron canadum), a species that can transition between marine and freshwater habitats, has also shown to be resistant to increased pCO2, because they have similar somatic growth rates when exposed to a range of pCO2 values (800 and 2100 µatm; Bignami et al. 2013). Second, it is possible that the feeding behaviours of freshwater fishes are not tightly linked to the potential physiological changes that fish undergo when exposed to elevated pCO2. As described above, in marine fishes, changes to the GABA neural-transmitter pathway are thought to be the mechanism by which behavioural changes occur in marine fish, and can be reversed if CO2-exposed fish are returned to ambient conditions. This pathway and feeding in freshwater fish exposed to elevated pCO2 have not been investigated and should be considered for future research, specifically in the context of rising aquatic pCO2, as not all marine fish species have had similar behavioural changes (Jutfelt and Hedgård 2013, 2015; Näslund et al. 2015; Sundin and Jutfelt 2016). Overall, no significant changes in feeding behaviours of M. salmoides were observed and this may be due to being exposed to elevated pCO2 during their evolutionary history and, potentially, because they have a more robust physiological response to high concentrations of CO2.

Prey item and other considerations

Although the focus of the current study was on the response of a predatory freshwater fish to CO2 exposure, our data also allowed us to make inferences related to the effect of CO2 on the prey fish in our study. The topic of how prey fishes respond following CO2 exposure has been quantified previously using marine fishes, and many studies have demonstrated that prey have reduced escape distances (Allan et al. 2013), longer reaction distances (Allan et al. 2013), impaired predatory detection (Dixson et al. 2010; Sundin and Jutfelt 2016), altered visual-risk assessment (Ferrari et al. 2012) and increased predation when exposed to elevated pCO2 (Ferrari et al. 2011). In fact, smaller freshwater fish have been found to have lower ventilation rates (an indication of sedation; Kates et al. 2012), along with impaired predator learning (Leduc et al. 2004) when exposed to elevated pCO2, which would presumably make them prone to consumption. In the present study, prey fish were not monitored for activity, but, presumably, if prey fish used in the present study were experiencing behavioural changes from the short-term exposure to elevated CO2, it would be expected that M. salmoides acclimated to ambient conditions (i.e. no change in pCO2) would have had higher consumption rates in the two treatments where pCO2 was elevated, which was not observed. Future studies should monitor behaviour and activity of prey fish to gain a clearer picture of how elevated pCO2 potentially may change predator–prey dynamics of freshwater fishes, which could have both synergistic and antagonistic effects (Ferrari et al. 2015).

Further to understanding the predator–prey dynamics of freshwater fishes, it is important to understand the role that CO2 plays in the ecology of freshwater systems. Similar to the marine environment, freshwater CO2 is expected to increase in some systems in the future, including the Laurentian Great Lakes (Phillips et al. 2015; Pichler et al. 2015), but future changes in pCO2 will vary widely on the basis of several environmental factors, including terrestrial primary productivity, substrate and biological respiration (Hasler et al. 2016a). In addition to changing concentrations of CO2 in fresh water, pCO2 may also become more variable in the future as a result of changing precipitation patterns (Butman and Raymond 2011), and could be altered because of management activities such as the installation of CO2 barriers (Noatch and Suski 2012). Together, in many freshwater systems, biota will likely be exposed to higher and variable CO2 concentrations. Data from the current study would suggest that there is minimal effect of elevated pCO2 on the feeding behaviour of M. salmoides.

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