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A Stochastic Trout Population Model for Supporting Fish Management

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Abstract: Brown trout (*Salmo trutta fario*) is an ecologically and economically important fish species in many Swiss rivers. Since the 1980s, a significant decrease of brown trout catches was reported across Swiss rivers. To better understand the causes of this decline, a trout population model was developed a few years ago. It predicted trout densities at single river reaches. We improved this model to better guide management decisions for river restoration. We extended the model by distinguishing stocked and resident fish. This allows us to account for the empirical evidence of different behavior of stocked and resident fish in order to better consider the effect of the most important fish management practice, stocking. We use different mortality rates for stocked and resident fish populations by introducing a mortality rate ratio between stocked and resident fish as a model parameter. The impact of this parameterization is studied by sensitivity analyses of the deterministic fry survival submodel as well as the full, stochastic brown trout life cycle model.

Keywords: Fish; Stocking effect; Population viability

1 INTRODUCTION

Because Brown trout (*Salmo trutta fario*) is a good indicator of the health of a river it is an ecologically important fish species in Swiss rivers. Moreover it presents a high recreational value. In Switzerland the record of angler catches decreased by 80% since 1960 [Fischnetz, 2004]. Several reasons for this phenomenon were suggested, from poor water quality, altered habitat, increase of fine sediment load, diseases, increased temperature, increased predation by birds, poor fish management practice to decreased angler activity [Burkhardt-Holm et al., 2005]. One of those was an unadapted fish management practice by intensive stocking. To help assess the causes and cost of different management alternatives, a full, stochastic life-cycle model was developed and presented by Borsuk et al. [2006].

For recreational purposes, fishery managers introduced in 2001 around 75 million fry in the Swiss river net [Fischnetz, 2004]. Evidently, stocking affects the density and distribution of brown trout populations. However, recent studies showed that stocking may not be always successful in increasing the population size [Araki and Schmid, 2010]. The stocked fish could even lead to an ecological competition between stocked and resident fish inducing a density-dependent mortality, which can lead to a reduction of the resident population abundance as reported by Baer and Brinker [2008]. Another concern is the

deterioration of the gene composition of the locally adapted population (leading to a loss in fitness) [Araki et al., 2007, 2009] and reduction of the genetic diversity of the resident population [Hansen et al., 2009]. Moreover, a lower fitness and reproductive capability of the stocked populations was shown in certain conditions [Hansen, 2002]. With the help of a simple population dynamical model including a gene hybridization between resident and stocked population and a density-dependent mortality, Satake and Araki [2012] showed that most stocked juveniles would not survive to maturation if they are subject to density-dependent competition.

In order to include this effect in the modified dynamic life-cycle model based on Borsuk et al. [2006], we extended it to handle separately the resident and stocked populations. To account for a possible lower fitness of the stocked population [Holzer et al., 2003; Peter, 1987], we can set a higher mortality rate for the stocked fish. We will here analyze the results of this parameterization for the deterministic fry survival submodel and for the full, stochastic life-cycle model simulating a real river reach for different values of mortality rates.

2 METHOD

We developed a parameterization for the survival of resident and stocked fish till the end of the first winter. To save space, we present here only the parameterization for the survival of the brown trouts till the end of summer, the survival from end of summer to end of next winter is similar, only the choice of the density-dependent mortality rate function is different. For this study, only the stocking of 0+ brown trout in spring is considered, which is subject to density-dependent competition.

2.1 Late summer fry density with the use of different mortality rates for stocked and resident brown trouts

Ricker curve for total fry. It has been shown that the brown trout late summer fry density, N_0 [ind ha⁻¹], can be described by a Ricker curve of density dependence $N_0 = r_f N_{\text{efry}} \exp(-b N_{\text{efry}})$ where r_f is the survival rate at low density, $b = r_f / (e K_f)$, K_f is the maximum recruitment capacity [ind ha⁻¹], and N_{efry} [ind ha⁻¹] is the fry density after emergence [Elliott, 1994]. We assume that the sum of both stocked and resident brown

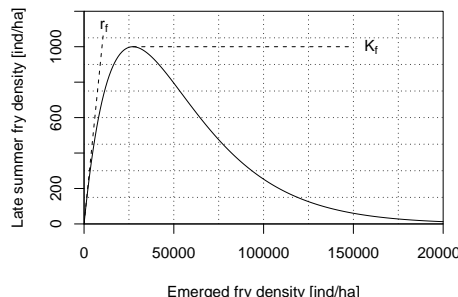


Figure 1: Example of a Ricker curve with $r_f=10\%$ and $K_f = 1000$ ind ha⁻¹.

trout are subject to this density-dependent mortality rate function (Ricker curve, illustrated on Fig. 1):

$$N_0^{\text{tot}} = r_f N_{\text{efry}}^{\text{tot}} \exp\left(-\frac{1}{e} \frac{r_f}{K_f} N_{\text{efry}}^{\text{tot}}\right) \quad (1)$$

with

$$\begin{aligned} N_0^{\text{tot}} &= N_0^{\text{resident}} + N_0^{\text{stocked}} : \text{total (resident + stocked) density of late summer fry [ind ha}^{-1}\text{]} \\ N_{\text{efry}}^{\text{tot}} &= N_{\text{efry}}^{\text{resident}} + N_{\text{efry}}^{\text{stocked}} : \text{total (resident + stocked) density of emerged fry [ind ha}^{-1}\text{]} \end{aligned}$$

Mortality rates. We compute the densities of resident and stocked trout separately. We assume the ratio of the mortality rates of stocked and resident trout to be constant (with respect to the densities of each population) and define it as a model parameter, f_{mort} :

$$f_{\text{mort}} = \frac{\text{mortality rate of stocked fishes } (N_{\text{efry}}^{\text{stocked}}, N_{\text{efry}}^{\text{resident}})}{\text{mortality rate of resident fishes } (N_{\text{efry}}^{\text{stocked}}, N_{\text{efry}}^{\text{resident}})} = \text{const} \quad (2)$$

The survival rate, c , of resident emerged fry then depends on both population densities of resident and stocked emerged fry, $c(N_{\text{efry}}^{\text{stocked}}, N_{\text{efry}}^{\text{resident}})$. The survival rate of stocked emerged fry is then equal to $c^{f_{\text{mort}}}$. This leads to densities of resident and stocked late summer fry given by:

$$N_0^{\text{resident}} = N_{\text{efry}}^{\text{resident}} \cdot c \quad (3)$$

$$N_0^{\text{stocked}} = N_{\text{efry}}^{\text{stocked}} \cdot c^{f_{\text{mort}}} \quad (4)$$

The system of Eqs. (1), (3) and (4) is solved numerically for N_0^{resident} , N_0^{stocked} and c given $N_{\text{efry}}^{\text{resident}}$, $N_{\text{efry}}^{\text{stocked}}$, r_f , K_f and f_{mort} .

For the survival of the fish over the following autumn and winter, we use the same procedure, but the density-dependent mortality rate has a hockey stick shape (total number 1+ fish at the end of winter is proportional to the total density of late summer fry till the maximal capacity is reached). A stocked brown trout is considered to have a higher mortality rate as a resident till the end of the first winter. In this study, f_{mort} is considered constant till the end of the first winter (even if the stocking occurred in spring).

Fry survival at low density r_f . The emerged fry survival rate at low density r_f of the total (resident + stocked) emerged fry population is defined to be consistent with the individual survival rates of resident and stocked populations:

$$r_f = \frac{N_{\text{efry}}^{\text{resident}}}{N_{\text{efry}}^{\text{resident}} + N_{\text{efry}}^{\text{stocked}}} \cdot a + \frac{N_{\text{efry}}^{\text{stocked}}}{N_{\text{efry}}^{\text{resident}} + N_{\text{efry}}^{\text{stocked}}} \cdot a^{f_{\text{mort}}} \quad (5)$$

where a is the survival rate of resident emerged fry at low density. This guarantees that mortality rates of purely resident or stocked populations differ by the factor f_{mort} .

3 RESULTS

We first analyze the direct effect of this parameterization on the deterministic fry survival submodel. Second, we extended the model described by Borsuk et al. [2006] by distinguishing the resident fish from the stocked populations and their different mortality rates. The full, stochastic life cycle model can show the possible feedbacks on the recovery of the population.

3.1 Analysis of the behavior of the deterministic fry survival model

We choose a maximum recruitment capacity of $K_f = 1000$ fish per hectare and a resident emerged fry survival rate at low density of $a = 10\%$. The densities of total, resident, and

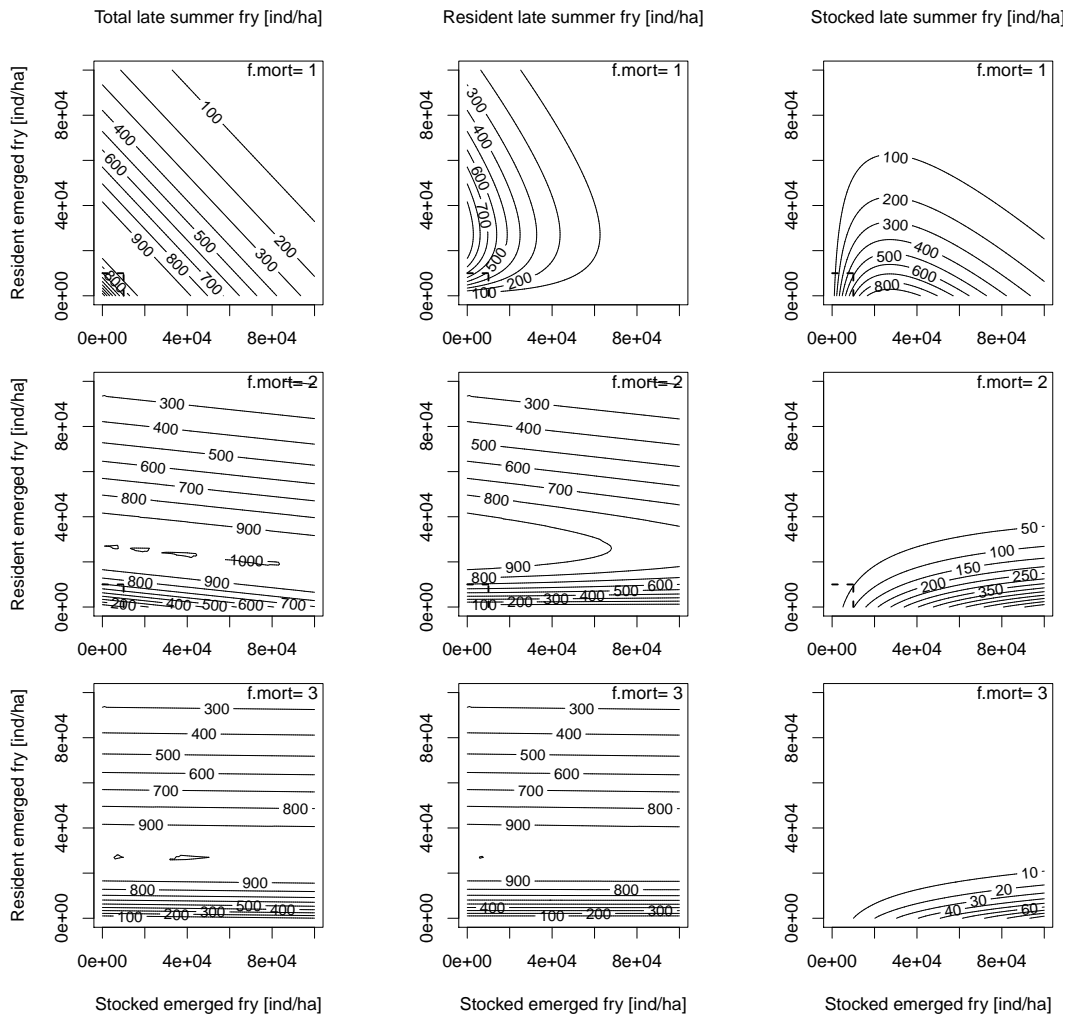


Figure 2: Illustration of the density of late summer fry [ind ha^{-1}] at the end of the summer with $K_f = 1000$ [ind ha^{-1}] and $a = 10\%$. The left, middle and right panels are, respectively, densities of total, resident and stocked late summer fry. The upper, middle and lower panels show the results for values of f_{mort} of 1, 2 and 3.

stocked late summer fry are shown in Figs. 2 and 3 as functions of stocked and resident emerged fry for different values of f_{mort} .

First, let's look at the basic case $f_{\text{mort}} = 1$, i.e. the mortality rate of stocked fry is the same as the one of resident fry (top panel in Figs. 2 and 3). The total density of late summer fry depends only on the sum of the densities of resident and stocked emerged fry. Increasing the number of resident emerged fry has exactly the same effect as increasing the number of stocked emerged fry on the total late summer fry density. For low densities, stocking leads to an increase in the total late summer fry population, while for higher total emerged fry density, stocking leads to a decrease in the total late summer fry density in the reach (see also Fig. 1).

In the opposite extreme case, when the mortality of the stocked emerged fry is set to be three times the mortality of the resident emerged fry ($f_{\text{mort}} = 3$), the stocked fry are dying

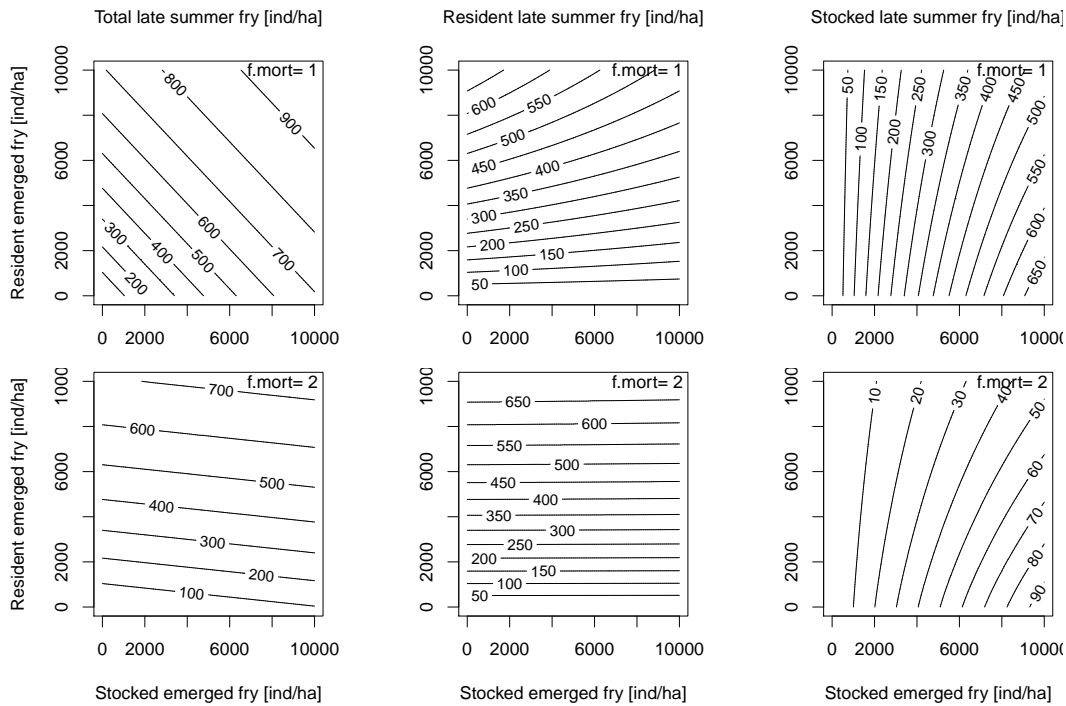


Figure 3: Zoom of the lower left corner of the upper two panels of Fig. 2 for small numbers of emerged fry (area delimited by dashed lines).

massively and have a very small impact on the total number of late summer fry (see the bottom panel of Fig 2). The pattern of the total number of late summer fry displayed in Fig. 2 is almost independent of the stocked emerged fry density. Even if there are only stocked fish, only a very small fraction of them survive. In the intermediate case, for $f_{\text{mort}} = 2$, we can see an intermediate behavior (middle row in Fig. 2, bottom row in Fig 3).

While an increase of f_{mort} induces an increase in the resident surviving fry and a decrease in the number of surviving stocked fish at the end of summer (instead for very high stocking densities), the impact on the density of total surviving fry depends on the initial density of emerged fry. For high density of stocked or resident emerged fry, a higher f_{mort} induces a higher total density of late summer fry. On the other hand, for small densities of emerged fry, it induces a decrease in the surviving total density of late summer fry as can be seen in Fig. 3.

Finally, in all the cases presented, for a given density of resident emerged fry, increasing the density of stocked emerged fry always decreases the density of resident late summer fry. On the opposite, increasing the density of resident emerged fry for a given density of stocked emerged fry leads to a smaller density of stocked late summer fry.

3.2 Impact of the parameterization in a full brown trout life-cycle model

We use here the model described by Borsuk et al. [2006] with the parameterization described in Section 2. This model simulates the whole life cycle of brown trout using expert knowledge to characterize the uncertainty of model parameters. Monte Carlo simulations

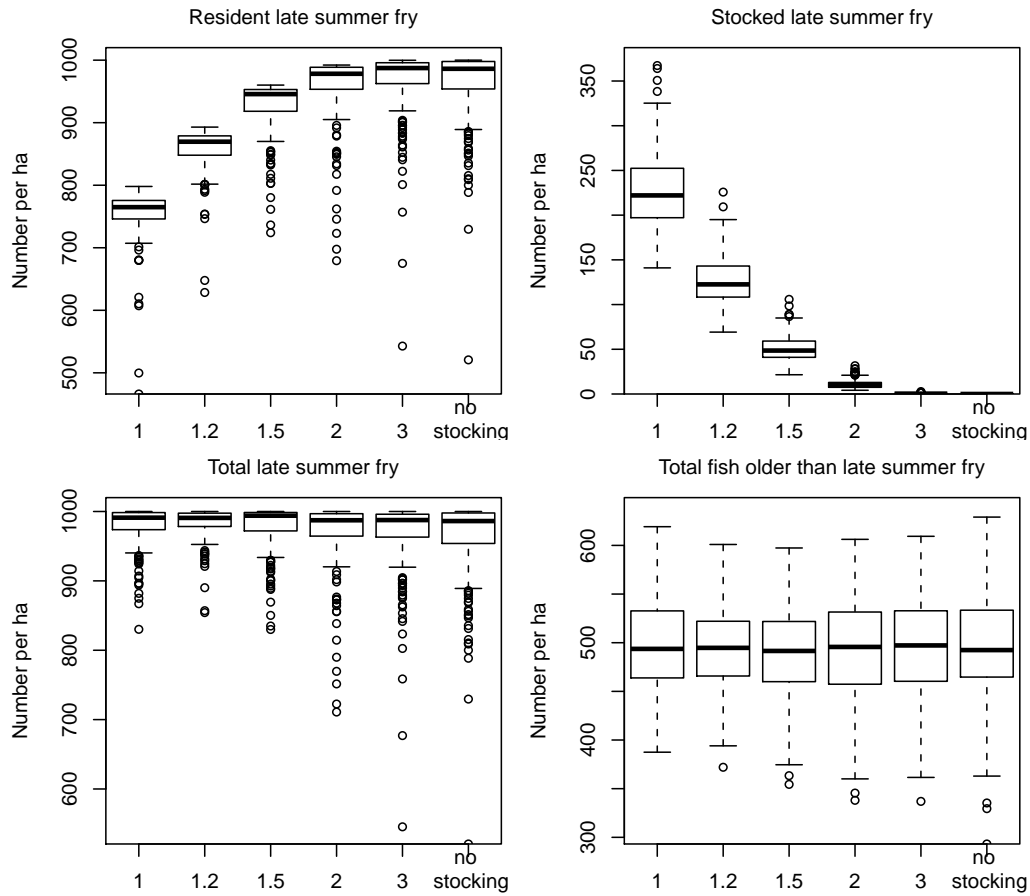


Figure 4: Box-plot of the number of brown trout per hectare in the simulated river reach for different fractions of the mortality rate ($f_{\text{mort}} = 1, 1.2, 1.5, 2$ and 3). Upper panels: resident and stocked late summer fry densities, lower panels: total density of late summer fry and total density of brown trout older than late summer fry.

propagate this uncertainty numerically through the model and account of stochasticity in time evolution. The age-structured population model is divided into the following life stages : egg, emerged fry, late summer fry, and the following year of life ($1+, 2+, 3+, \dots$). Each transition from one life stage to the next one include the influence of natural and anthropogenic factor, as gravel bed condition, water quality, water temperature, habitat conditions, etc. Most of the parameters describing the latter effects are represented with conditional probability distributions.

The simulations presented here are designed for an upstream reach of the river Lützelurmurg situated in north-eastern Switzerland. The reach has about 2.6 m of wetted width and the length of the considered river reach is 159 m. The river section has a sustained resident population. The spawning and incubation success are high, the percentage of fine particles is only 4%. For an easy comparison with Section 3.1, the maximum recruitment capacity is set to be 1000 individuals per hectare. The survival rate of resident emerged fry at low density is described by the same symmetric triangular distribution as in Borsuk et al. [2006] (mode 0.09, lower bound 0.08, upper bound 0.1). We introduce 320 stocked emerged fry into the reach (≈ 7600 emerged fry per hectare) in early spring of each year. This density of stocking is representative of the actual stocked

densities in Switzerland (on average one brown trout is stocked per meter of swiss river [Fischnetz, 2004]). Fig. 4 shows a sensitivity analysis with no stocking and with different ratios of the mortality rates of stocked to resident fry. Each simulation is run for 200 years, the first 10 years being removed from the analysis.

First, we can see that in the lower panels of Fig. 4 showing the total density of late summer fry and fishes older than 6 months, none of the simulations including stocking show an increase of fish compared to the simulation without any stocking. This is resulting from the values of stocking and simulated resident emerged fry (around 30 000 fish per hectare). In Fig. 2, we saw that an increase of f_{mort} can induce a higher or lower total surviving density in autumn. The emerged densities in this simulation correspond to the range where f_{mort} has only a small effect on the total late summer fry density.

The total late summer fry density without stocking tends to the maximum recruitment capacity K_f . This comes from a stable state of the simulated system, in which the simulated late summer fry density is proportional to the maximum recruitment capacity. The proportionality factor is in the presented simulation around 1 because of the parameter choice for the survival rates from one age-class to the following. The stable simulated late summer fry density can be smaller than the maximum recruitment capacity with other parameter choice.

If stocking could appear not to be harmful in term of total population, there is no interest in stocking in terms of resident fish. The more stocked fry is surviving, the more resident die. Only a value of 2 or 3 for f_{mort} gives a similar behavior as if there would be no stocking, the majority of stocked fry dying very quickly. For low mortality rate fractions, the resident population decreases, implying a loss in resident gene pool as the stocked fry are surviving.

If the mortality rate of stocked fry is equal to the one of the resident population ($f_{\text{mort}}=1$), we observe the smaller surviving of resident fish, as the stocked population density is larger and is consequently using more resources. If the mortality rate fraction increases, more stocked fry are dying, inducing less competition for resident fry. The higher the mortality rate fraction, the less effect the stocking has on the resident population.

4 CONCLUSIONS

Based on the reported lower fitness of stocked brown trout, we implemented a simple parameterization distinguishing stocked and resident mortality rates in the whole stochastic life-cycle model presented by Borsuk et al. [2006]. We define a new parameter value f_{mort} , the factor by which the mortality of stocked fish is higher than that of resident fish. We present a sensitivity study with respect to different mortality rate ratios between stocked and resident fry in a river with successful natural reproduction of the resident population. We used a 'typical' stocking related to the actual average value of stocking density in Switzerland. For the surviving of resident fry, stocking has no effect for large values of f_{mort} , but reduces the density of surviving residents for small values of f_{mort} (smaller than 2). Our simulations indicate no increase of total adult fish density due to stocking in a river section with naturally sustainable resident population. In the same river section with smaller natural reproduction, e.g. due to inadequate habitat condition, stocking can lead to an increase of the total adult population.

By doing the same simulations with higher stocking value (for example 5000 emerged fry per year for this reach), Fig. 4 becomes quite different (not shown). Stocking has then a much higher effect on resident late summer fry densities, possibly leading to an extinction. The results of the full life cycle model shown and discussed here is thus valid

for middle stocking values with respect to the maximum recruitment capacity, but it cannot be concluded that stocking has a small influence on the total late summer fry level or any particular conclusion. This stocking model, which needs some evaluation and validation, could be used for optimizing the amount of stocked fish in the rivers.

This study does not include migration of brown trout between different river reaches. This is an important process which should be taken into account. This could induce re-colonization and other feedbacks. We will extend our model to a meta-population model that accounts for fish migration.

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