

Habitat choice of the invasive *Gammarus tigrinus* and the native *Gammarus salinus* indicates weak interspecific competition

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Following the establishment of the invasive gammarid amphipod *Gammarus tigrinus* the native gammarids almost disappeared from some habitats of the northeastern Baltic Sea. The aims of the current work were to experimentally study whether the habitat choice of *G. tigrinus* and *G. salinus* was similar and whether *G. tigrinus* modified the habitat selection of *G. salinus*, providing thus evidence that competition for space between the two species might explain the disappearance of the native gammarids from the study area. In general, the gammarid amphipods had a significant overlap in habitat selection. Gammarids modified the habitat choices of co-occurring species but impacts were disproportional among species. The effects of *G. tigrinus* on *G. salinus* were stronger than vice versa. However, the effects varied among months, and the negative responses were not observed in all habitats. Thus, competition for space alone cannot explain the mass disappearance of the native *G. salinus*.

Introduction

Macroalgae are among the primary habitat providers across shores worldwide. Consequently, interactions between macroalgae and associated invertebrates are important areas of research in ecology (e.g. Schiel 2004). Species are patchily distributed, which suggests that their distribution pattern is a result of habitat selection (e.g. Underwood *et al.* 2004). Whether qualitative (plant identity) and/or quantitative (total plant biomass) plant traits structure the faunal assemblages depends very much on if associated fauna dominated by habitat (resource) specialists or generalists (Parker *et al.* 2001).

Gammarid amphipods are ranked among the most important necto-benthic herbivores in many coastal seas. They are found on vegetated areas; however, the knowledge on their habitat selection is scarce (e.g. Pavia *et al.* 1999, Van Overdijk *et al.* 2003, Kraufvelin *et al.* 2006, Vandendriessche *et al.* 2006, Duggan and Francoeur 2007). Earlier observations have indicated that gammarids choose their habitat according to the dimensions of the hiding place within stone fields, algae and mussel beds in order to get protection from predators and/or mechanical disturbance due to waves (Fenchel and Kolding 1979). On the other hand, the selection is related to the quality and quantity of food (Kinne 1959). Other

studies have shown that gammarids are not habitat specialists (MacNeil *et al.* 1999) and the biomass of macrophytes predicts well the density of gammarids (Costa and Costa 1999, Kraufvelin *et al.* 2006, Duggan and Francoeur 2007).

The Baltic Sea has low taxonomic and functional diversity (Bonsdorff and Pearson 1999) and each ecosystem function is often represented by a few species. Thus, the loss or addition of a species may correspond to the loss or addition of an ecosystem function. Only five native gammarid species are found in the northeastern Baltic Sea: *Gammarus locusta*, *G. oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni* (Hällfors *et al.* 1981). These species have different habitat requirements, although with a significant overlap. So, *G. locusta*, *G. oceanicus* and *G. salinus* prefer deeper sites than *G. duebeni* and *G. zaddachi*. As compared with *G. salinus*, *G. locusta* and *G. oceanicus* inhabit more exposed areas. Where *G. duebeni* and *G. zaddachi* coexist, there is in general a clearcut vertical zonation with *G. duebeni* inhabiting just the water's edge and *G. zaddachi* deeper down (Vader 1977, Kolding 1981, Kotta *et al.* 2000a).

The nonindigenous amphipod *G. tigrinus* was first found in the northern Baltic Sea in 2003 (Herkül and Kotta 2007). Within a few years, the species considerably expanded its distribution area and became a dominant member of gammarid amphipods. Following the establishment of *G. tigrinus* the densities of native gammarids, especially of *G. salinus*, were severely declined (Herkül *et al.* 2009). Similar results have earlier been reported from other parts of the Baltic Sea and different freshwater systems (e.g. Pinkster *et al.* 1992, Jazdzewski *et al.* 2002, Grabowski *et al.* 2006). Because no manipulative experiments have been made, we are not able to conclude whether the decrease in native amphipods was due to the competitive interactions between gammarids or other factors (e.g. changes in macrophyte assemblages). Nevertheless, the field data indicate a lack of any pronounced shift in the macroalgal community structure in the northeastern Baltic Sea during the 2000s (HELCOM 2009). Similarly, coastal fishes, that may exert a significant pressure on the mesoherbivore communities (Menge and Sutherland 1976), did not increase their densities in the study area. Instead,

an excess growth of filamentous algae may result in reduced viability of fish populations (e.g. Candolin *et al.* 2006).

Therefore, the aims of this paper were to experimentally investigate (1) whether *G. tigrinus* occupies same habitat as the native gammarid *G. salinus*, and (2) whether the presence of *G. tigrinus* modifies the habitat selection of *G. salinus* and vice versa. Our hypotheses were that (1) the habitat requirements of *G. salinus* and *G. tigrinus* are similar; (2) however, because of the aggressive behaviour of the invasive species (Kinzler and Maier 2003), *G. salinus* has a wider range of habitat selection without *G. tigrinus* than with *G. tigrinus*.

Material and methods

The study was conducted on the shore of the shallow semi-enclosed Kõiguste Bay (58°21'N, 22°59'E), Gulf of Riga, northeastern Baltic Sea. Kõiguste Bay is characterized by sandy clay bottoms mixed with gravel or boulders. The prevailing depths are between 1 and 4 m. A huge drainage area supplies the Gulf of Riga with fresh water, which mostly enters the southern part of the basin. The average salinity of Kõiguste Bay varies from 4 to 6. As the bay is shallow, the dynamics of water temperature is directly coupled with air temperatures. In a normal year Kõiguste Bay has an ice cover until late April. In May the water temperature quickly rises to about 17–20 °C. In the course of autumn storms in September–October the surface water cools down to 5–10 °C. The oxygen regime is relatively good due to strong vertical mixing (Kotta *et al.* 2008a and references therein). The benthic vegetation is well developed and extensive proliferation of ephemeral macroalgae has been reported from the area in recent years (Paalme *et al.* 2004, Lauringson and Kotta 2006).

Habitat choice experiments were performed in May, July and September 2005. The macrophyte species used in the experiments reflected their seasonal occurrence in the field (Table 1). Macrophytes were collected from a shallow (1–3 m) area adjacent to Kõiguste Marine Biological Laboratory. Seven different macrophyte species were used in the habitat choice experiments: the brown

algae *Fucus vesiculosus* and *Pylaiella littoralis*, the red algae *Ceramium tenuicorne* and *Furcellaria lumbricalis*, the green algae *Cladophora glomerata* and *Ulva intestinalis*, and the higher plant *Myriophyllum spicatum*. The amphipods *G. tigrinus* and *G. salinus* were collected from the same site either from under the stones by means of a handnet or from within the stands of perennial macrophytes by shaking the algae. Only adult specimens were used in the experiment. The perennial algae *F. vesiculosus* and *F. lumbricalis* were not found in spring due to the intensive ice scour during the previous winter.

The habitat choice experiments were performed in 100 l aquaria with a light regime similar to the field conditions. During the experiment the daylight hours were from 05:00 to 21:00 in May, from 04:30 to 22:00 in July and from 07:00 to 19:00 in September. The aquaria received running seawater at a flow rate of 3 l h⁻¹. The water was taken from 2-m depth near the Kõiguste Marine Biological Laboratory. Water temperature was estimated at 15 °C in May, 23 °C in July and 12 °C in September. Stones around 5 cm in diameter, all available macrophyte species and either 10 *G. salinus*, 10 *G. tigrinus* or the mixture of 5 specimens of *G. salinus* and 5 specimens of *G. tigrinus* were added to each aquarium. All treatments were replicated three times. The amphipod densities used in this study reflected their natural values in the field. Prior to the experiment, the gammarid amphipods were determined to species level. In order to do so, each individual was gently placed on a petri dish by using a small piece of nylon mesh and inspected within a small amount of water under a binocular microscope. Besides microscopic features, *G. tigrinus* was characterized by conspicuous stripes as opposed to the

uniform coloured of *G. salinus*. The algae were attached to the aquarium floor by stones. Each macrophyte species was placed in the aquaria as a single patch. The coverages of algae and stones in the aquaria were 20% and 10%, respectively, resembling the real values in field conditions.

Each month, the number of gammarids on different macrophytes, under stones and those swimming freely were recorded every hour for 30 h. During the dark periods, artificial red light was used for observations. No gammarids were clinging to the walls of the aquaria and no copulating specimens were observed in our experiment. The low coverages made it possible to see through macrophytes and the occurrences of gammarids within macrophytes could be recorded without disturbing the animals. As the survival of gammarids in the habitat choice experiments was 100%, it was assumed that all gammarids not associated to macrophytes or swimming freely hid under the stones.

Repeated measures ANOVA was used to compare the effects of identity of gammarid species (levels: *G. salinus*, *G. tigrinus*) and number of gammarid species (levels: one, two species; i.e. the single species treatments include either *G. salinus* or *G. tigrinus* and the two-species treatments include both *G. salinus* and *G. tigrinus*) on the habitat choice of gammarids among habitat types (levels: stones, swimming, *F. vesiculosus*, *P. littoralis*, *C. tenuicorne*, *F. lumbricalis*, *C. glomerata*, *U. intestinalis*, *M. spicatum*), light levels (levels: daytime, dark) and different months (May, July, September). A post-hoc Bonferroni test was used to analyse which treatment levels were statistically different from each other. Repeated measures ANOVA is more appropriate here than standard ANOVA because e.g., the habitat choice may violate the ANOVA independence assumption. This condition is unlikely to be met when the treatment observations are made simultaneously whereas repeated measures ANOVA explicitly accounts for these within-block correlations (Lockwood 1998).

Table 1. Macrophyte species used in the habitat choice experiments in different months.

Macrophyte species	May	July	September
<i>Fucus vesiculosus</i>		+	+
<i>Pylaiella littoralis</i>		+	
<i>Ceramium tenuicorne</i>			+
<i>Furcellaria lumbricalis</i>		+	+
<i>Cladophora glomerata</i>		+	
<i>Ulva intestinalis</i>	+	+	+
<i>Myriophyllum spicatum</i>	+	+	+

Results

Except for light and gammarid species, all studied factors had a separate significant effect on the

habitat choice of gammarids. Besides, all factors interactively affected the choices (Table 2). The gammarid amphipods had a significant overlap in habitat utilization but there were also some differences among the gammarid species. During the daytime, *G. salinus* were more attracted to macrophytes as compared with *G. tigrinus* (post-hoc Bonferroni test for the majority of macrophyte species: $p < 0.01$). The occurrence of *G. tigrinus* on stones exceeded the values of *G. salinus* in July and September ($p < 0.001$) but not in May ($p > 0.05$). In the daytime only a few *G. salinus* but none of *G. tigrinus* were swimming

($p < 0.001$). During the dark period, however, such differences were much weaker. Neither *G. salinus* nor *G. tigrinus* largely discriminated among the studied macroalgae, and the swimming activity of amphipods did not vary between the species (Figs. 1 and 2).

Gammarids modified the habitat choices of co-occurring species, but the impacts were disproportional among species. The effects varied among months and the negative responses were not observed in all habitats. The invasive *G. tigrinus* had stronger effects on the native *G. salinus* than vice versa. The invasive *G. tigrinus*

Table 2. Multivariate tests of significance of repeated measures ANOVA to compare the effects of identity of gammarid species (factor levels: *G. salinus*, *G. tigrinus*) and number of gammarid species (factor levels: one, two species; i.e. the single species treatments include either *G. salinus* or *G. tigrinus* and the two-species treatments include both *G. salinus* and *G. tigrinus*) on the habitat choice of gammarids among habitat types (levels: stones, swimming, *F. vesiculosus*, *P. littoralis*, *C. tenuicorne*, *F. lumbricalis*, *C. glomerata*, *U. intestinalis*, *M. spicatum*), light levels (levels: daytime, dark), and different months (levels: May, July, September). Habitat types, light levels and months are considered as repeated measures. Significant effects are set in boldface.

Factor	SS	df	MS	F	p
Gammarids	0	1	0	1.16	0.297
Sp. no.	0	1	0	4.91	0.042
Gammarids × Sp. no.	0	1	0	1.62	0.221
Month	0	2	0	324.65	< 0.001
Month × Gammarids	0	2	0	2.93	0.068
Sp. no. × Month	0	2	0	1.61	0.215
Gammarids × Sp. no. × Month	0	2	0	0.45	0.642
Light	0	1	0	0.61	0.448
Gammarids × Light	0	1	0	0.03	0.874
Sp. no. × Light	0	1	0	0.33	0.575
Gammarids × Sp. no. × Light	0	1	0	0.30	0.594
Habitat	285663	8	35708	227.25	< 0.001
Gammarids × Habitat	18977	8	2372	15.10	< 0.001
Sp. no. × Habitat	2121	8	265	1.69	0.108
Gammarids × Sp. no. × Habitat	1168	8	146	0.93	0.495
Month × Light	0	2	0	0.26	0.776
Gammarids × Month × Light	0	2	0	0.83	0.447
Sp. no. × Month × Light	0	2	0	0.33	0.719
Gammarids × Sp. no. × Month × Light	0	2	0	0.22	0.803
Month × Habitat	20052	16	1253	8.56	< 0.001
Gammarids × Month × Habitat	15976	16	999	6.82	< 0.001
Sp. no. × Month × Habitat	4855	16	303	2.07	0.010
Gammarids × Sp. no. × Month × Habitat	2213	16	138	0.94	0.518
Light × Habitat	69444	8	8681	41.83	< 0.001
Gammarids × Light × Habitat	13189	8	1649	7.94	< 0.001
Sp. no. × Light × Habitat	668	8	84	0.40	0.917
Gammarids × Sp. no. × Light × Habitat	784	8	98	0.47	0.874
Month × Light × Habitat	11651	16	728	5.00	< 0.001
Gammarids × Month × Light × Habitat	11158	16	697	4.79	< 0.001
Sp. no. × Month × Light × Habitat	2273	16	142	0.98	0.484
Gammarids × Sp. no. × Month × Light × Habitat	2697	16	169	1.16	0.304

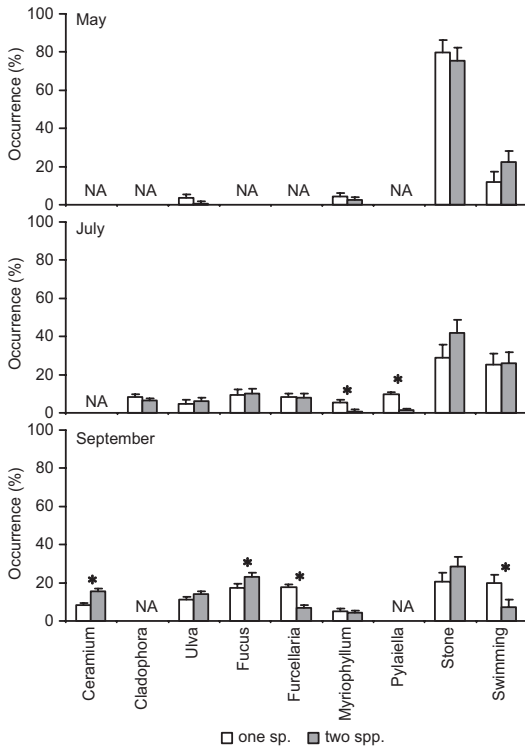


Fig. 1. Comparison of mean occurrence of *G. salinus* (+ SE) in different habitat types in single and two-species gammarid treatments during different months. The daytime and the dark period are pooled. The asterisks stand for a significant difference between the single species treatments and the two-species treatments in the habitat choice of gammarids (i.e. competition induced changes). NA denotes a lack of the named macrophyte species for the respective season (see also Table 1). Data were not transformed prior to the statistical analysis. The codes of the studied habitat types are as follows: Ceramium = *Ceramium tenuicorne*, Cladophora = *Cladophora glomerata*, Ulva = *Ulva intestinalis*, Fucus = *Fucus vesiculosus*, Furcellaria = *Furcellaria lumbricalis*, Myriophyllum = *Myriophyllum spicatum*, Pylaiella = *Pylaiella littoralis*, Stone = amphipods hiding under stones, Swimming = free-swimming amphipods.

significantly reduced the affinity of *G. salinus* to *M. spicatum* (post-hoc Bonferroni test: $p = 0.037$) and *P. littoralis* in summer ($p < 0.001$), and *F. lumbricalis* in autumn ($p < 0.001$) and increased the affinity of *G. salinus* to *C. tenuicorne* ($p < 0.001$) and *F. vesiculosus* in autumn ($p = 0.035$). Presence of *G. tigrinus* also resulted in a reduced swimming activity of *G. salinus* in autumn ($p = 0.031$). On the other hand, *G. salinus* significantly reduced the affinity of *G. tigri-*

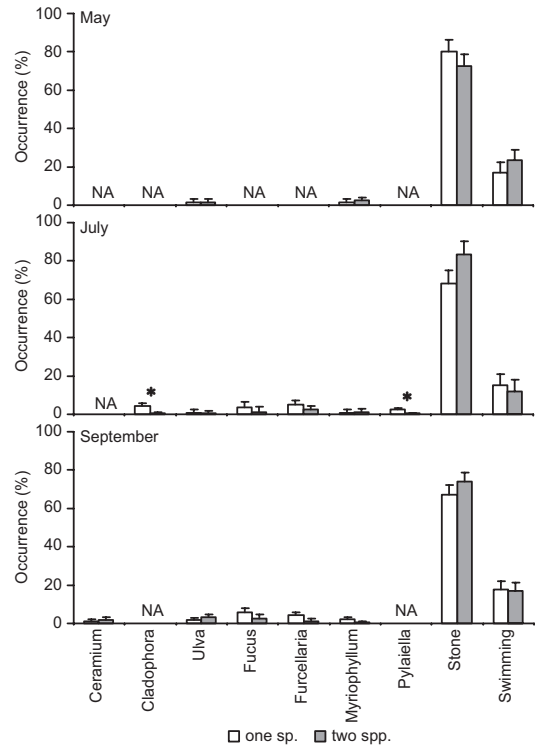


Fig. 2. Comparison of mean occurrence of *G. tigrinus* (+ SE) in different habitat types in single and two-species gammarid treatments during different months. The daytime and the dark period are pooled. The asterisks stand for a significant difference between the single species treatments and the two-species treatments in the habitat choice of gammarids (i.e. competition induced changes). NA denotes a lack of the named macrophyte species for the respective season (see also Table 1). Data were not transformed prior to the statistical analysis. The codes of the studied habitat types are as follows: Ceramium = *Ceramium tenuicorne*, Cladophora = *Cladophora glomerata*, Ulva = *Ulva intestinalis*, Fucus = *Fucus vesiculosus*, Furcellaria = *Furcellaria lumbricalis*, Myriophyllum = *Myriophyllum spicatum*, Pylaiella = *Pylaiella littoralis*, Stone = amphipods hiding under stones, Swimming = free-swimming amphipods.

nus to *C. glomerata* ($p = 0.012$) and *P. littoralis* in summer only ($p = 0.039$).

Discussion

The experiments partly supported the hypothesis that *G. tigrinus* and *G. salinus* have similar habitat requirements. Although the habitats of the studied gammarids largely overlapped, the

occurrence of *G. salinus* within macrophytes generally exceeded the values of *G. tigrinus* and the occurrence of *G. tigrinus* on the stones exceeded that of *G. salinus*. This agrees with the earlier findings of Van Riel *et al.* (2007) that *G. tigrinus* prefers mixed and small stones and the invasive gammarid species is less likely to swim as compared with the native species.

The study also demonstrated that neither *G. salinus* nor *G. tigrinus* discriminated among the studied macroalgae. The availability and quality of food and structural complexity of macroalgae are considered as universal mechanisms that determine the number of grazers in vegetated areas (Martin-Smith 1993, Hay 1996, Kotta *et al.* 2006). Owing to higher nutritional value annual species are more rewarding food than perennial species (Orth and Van Montfrans 1984, Pavia *et al.* 1999), but perennial species overgrown by epiphytes are especially favoured (Nicotri 1980, Duffy 1990, Boström and Mattila 1999). Moreover, such a combination provides grazers both protection from adverse conditions and a diverse feeding ground (Orav-Kotta and Kotta 2004). Although different types of macrophytes were available to amphipods within a relatively small spatial area in our experiment, the gammarid amphipods showed no or weak preference for certain macrophyte species. The lack of selection indicates that the habitat choice of gammarids is stochastic or not related to macrophyte species. Instead, gammarids may select for the (micro) epiphytic composition of vegetation (Jaschinski *et al.* 2009). This was also the reason why our experiment did not include juvenile gammarids. It is expected that owing to their high grazing efficiencies, small size and low swimming activity (Andersson *et al.* 2009), juveniles may find (epiphytic) food more important than shelter.

In harsh environments, however, grazers may trade feeding opportunities for habitat that provides better protection against waves, ice scour or predators (Gilliam and Fraser 1987, Main 1987, Schneider and Mann 1991). In our study, *G. tigrinus* had an extremely hidden mode of life as compared with the native *G. salinus*. Occasionally, *G. tigrinus* swam among algae during very short periods at night to utilize food sources. For the remaining period the gammarids hid under pebbles. We observed that *G.*

tigrinus was a faster swimmer than the native species. It is likely that in its native habitats *G. tigrinus* resists harsh and unstable conditions and tolerates high predatory pressure, and therefore hiding behaviour is favoured over swimming activity. This behavioural trait seems to be rewarding in the northern Baltic Sea where extreme weather events and intense ice or gravel scouring are relatively frequent and macrophytes are seasonally almost lacking in the shallowest coastal areas inhabited by *G. tigrinus* (Herkül *et al.* 2009).

In its native range the distribution area of *G. tigrinus* overlaps with some gammarid species that are also common in the Baltic Sea area. Nevertheless, because of differences in habitat selectivity, these species rarely co-exist (Steele and Steele 1972). In the Baltic Sea, however, many euryhaline species widen their ecological range due to low and stable salinities (Dahl 1973, Fenchel and Kolding 1979, Kolding 1981), and therefore *G. tigrinus* is found in the same habitats as *G. oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni*.

Following the invasion of *G. tigrinus*, *G. salinus* almost disappeared from Kõiguste Bay (Herkül *et al.* 2009). This suggests that *G. tigrinus* competes with *G. salinus* either for food or space. Our experiment did not support the hypothesis that in controlled experimental conditions *G. salinus* has a broader range of habitat selection without *G. tigrinus* than with *G. tigrinus*. Instead, our experiments demonstrated that *G. tigrinus* decreased the swimming activity of *G. salinus*. Such change in a behavioural trait, however, should have no negative consequences for the survival of the native gammarids as the probability of fish predation is likely to be reduced (Russo 1987).

Nevertheless, *G. tigrinus* significantly reduced the number of *G. salinus* within *P. littoralis*, *M. spicatum* and *F. lumbricalis*. In the northeastern Baltic Sea *P. littoralis* is by far the most dominant macrophyte species (Kotta and Orav 2001, Kotta *et al.* 2008b, Möller *et al.* 2009), and earlier studies have shown that this species is also the most rewarding food for mesoherbivores (Kotta *et al.* 2000b, Orav-Kotta and Kotta 2004). Therefore, despite the large quantities of food, aggression among gammarid

species may occur within *P. littoralis* habitats in summer and autumn. In this period *G. tigrinus* induces an elevated mortality on *G. salinus* within *P. littoralis* (Orav-Kotta et al. 2009). Namely, invasive gammarids are recognized as aggressive predators and they may prey heavily on native gammarids (Dick et al. 1993, Dick and Platvoet 2000, Kinzler and Maier 2003). Such aggression by the invasive *G. tigrinus* may force the native gammarids to leave their preferred habitats. Thus, the negative effects of *G. tigrinus* on *G. salinus* may actually explain the disappearance of native gammarids from some macrophyte habitats. However, as the effects varied among months and the negative responses were not observed in all habitats, competition for space alone cannot explain the mass disappearance of the native *G. salinus* from all studied macrophyte habitats. Besides, *G. tigrinus* is competitively inferior to some native species, e.g. *G. duebeni*, with *G. tigrinus* suffering heavy intraguild predation from *G. duebeni* (MacNeil and Prenter 2000).

To conclude, the habitat choice of *G. salinus* and *G. tigrinus* was broad and neither species discriminated largely between macrophytes. Although their habitat types overlapped in experimental conditions, *G. tigrinus* had only minor negative short-term effects on *G. salinus*. Thus, based on previous experimental evidence (Orav-Kotta et al. 2009), we may speculate that the negative effects of *G. tigrinus* on *G. salinus* in the northeastern Baltic Sea are due to the aggressiveness of *G. tigrinus* towards the native gammarids within the most rewarding macrophyte habitats.

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