

サウスシェトランド近海におけるナンキョクオキアミ *Euphausia superba* Danaの食習性

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Food habits of the Antarctic krill *Euphausia superba* Dana in South Shetland waters^{1,2}

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Abstract

Food habits of the Antarctic krill (*Euphausia superba*) in waters adjacent to the South Shetland Islands were investigated during the austral summer of 1991. A total of 74 krill collected at 20 stations were selected, and their foregut contents identified using an inverted light microscope. The foregut contents were almost exclusively members of the two diatom genera: *Nitzschia* and *Thalassiosira*. Differences in food composition were found between specimens collected at two station types, offshore and onshore. The foregut contents of the former showed a high percentage of the small chain-forming *Nitzschia*, whereas *Thalassiosira* and tintinnids were more frequent in the latter. Average concentrations of integrated chlorophyll-*a* in the upper 100-m water column were higher at all of the onshore stations than at any of the offshore stations, but there was little difference in the abundance of microzooplankton (naked ciliates and tintinnids) between the two station groups. Krill of juvenile and younger maturity stages (♂: II A, III A; ♀: II B, III A) were dominant at onshore stations while the advanced stages (♂: III B; ♀: III BC, III D, III E) were dominant at offshore stations. At onshore stations, where the younger and advanced stages were collected, the younger stages showed a tendency to be more omnivorous than the advanced stages. This suggests that *E. superba* changes its food habits ontogenetically as it progresses through the stages of sexual maturity. In short, the younger stages exhibit omnivorous trends, while the advanced stages show herbivorous feeding habits.

Key words: Antarctic krill, herbivore, omnivore, change of food habits

In light of the vast abundances of *Euphausia superba* and its pivotal role in linking primary production to various predators in the Antarctic food web, the feeding activities of *E. superba* have consequences of great importance for the understanding of the structure, function and management of Antarctic marine ecosystems (Laws 1985, Quetin & Ross 1985, El-Sayed 1990).

The feeding habits of *E. superba* are considered to essentially be herbivorous in contrast to other euphausiid species (Barkley 1940, Marr 1962, Mauchline & Fisher

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1969, Nemoto 1972, Kawamura 1981, Ligowski 1982, Miller & Hampton 1989), especially during the austral spring and summer when phytoplankton blooms. But in summer the succession of the phytoplankton species composition in the water column does occur, and every once in a while the biomass of microzooplankton and heterotrophic microflagellates exceeds that of phytoplankton and they have therefore been suggested to be an important alternative food resource for *E. superba* (Clarke 1985, Hews et al. 1985, Stretch et al. 1988, Boltovskoy et al. 1989). Feeding experiments suggest that *E. superba* ingests copepods more efficiently than phytoplankton (Price et al. 1988). *Euphausia superba*, under rearing conditions, sometimes exhibit cannibalism (McWhinnie et al. 1979, Miller 1982, Ishii et al. 1985). In South Georgian waters, the foregut contents of *E. superba* in winter were filled with the fragments of pereopods etc. of younger *E. superba* (Nishino & Kawamura 1994). The above mentioned evidence suggests that the food habits of *E. superba* during summer are more omnivorous than herbivorous. There are currently no reports as to the feeding habits of *E. superba* with respect to the stages of sexual maturity.

This study examines whether or not *E. superba* change their feeding habits in accordance with variations in ambient food concentrations and type or with differing sexual maturity stages.

Materials and Methods

Antarctic krill (*Euphausia superba*) were collected during the 6th Antarctic Expedition (Nov. 1990–Mar. 1991) of the R/V Kaiyo Maru of the Japan Fisheries Agency in the vicinity of the South Shetland Islands. We refer to sampling stations located in waters shallower than 500 m “onshore” stations and those deeper than 500 m “offshore” stations (the mean depth of 7 onshore stations was 275 m, that of 13 offshore stations was 3657 m). *Euphausia superba* specimens investigated in this study were collected at 20 stations with a KYMT net (Kaiyo Maru Midwater Trawl; mouth area of 9 or 7.3 m², mesh aperture of 3.4 mm) in the northern waters of the Antarctic Peninsula extending from Elephant Island to Livingston Island from 18 January to 3 February 1991 (Figure 1). The net was towed obliquely, from 100 m to the surface, at a ship’s speed of 3 knots. The foreguts of *E. superba* individuals were dissected out immediately after sampling and preserved in 1% glutaraldehyde in the ship’s laboratory. The foregut contents were immersed in filtered seawater to identify and count easily and observed using an inverted light microscope. A total of 74 krill individuals were analyzed for foregut contents (Table 1). All *E. superba* specimens collected were examined and analyzed by sexual maturity stage according to the method of Makarov & Denys (1981). A 500-ml surface seawater sample was collected using a sampling bucket at the stations where *E. superba* were collected with the exception of three stations (Sts. 115-2, 129-2 and 143-2), and was preserved in 1% glutaraldehyde.

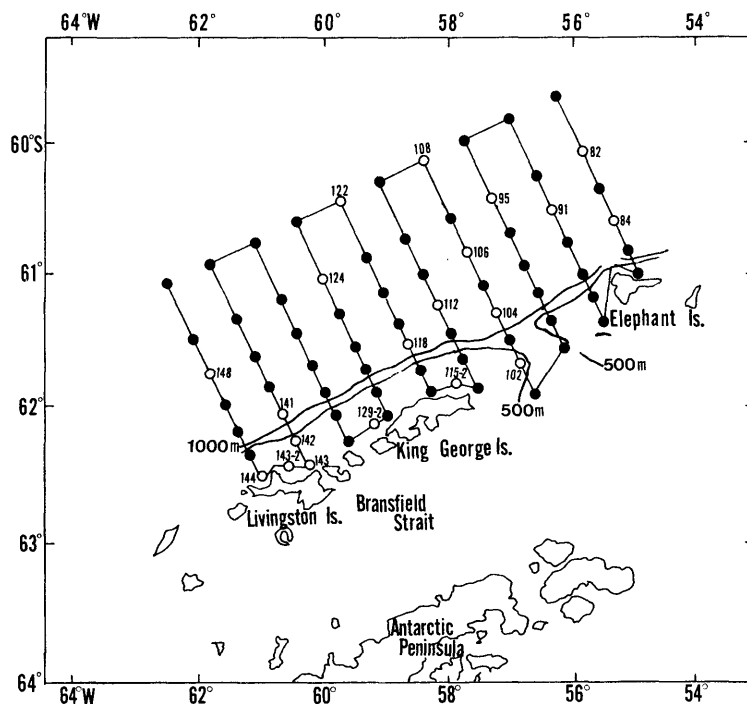


Fig. 1. Hydrographic stations in Leg II of the 6th Kaiyo Maru expedition. *E. superba* examined in this study were collected at the 20 stations which are designated with open circles. (After Fisheries Agency 1993)

Table 1. Sexual maturity stages and number of *E. superba* used for foregut content analysis. The upper and lower sections indicate offshore and onshore stations, respectively.

Sampling Station	Sexual maturity stages							
	♂ II A	♂ III A	♂ III B	♂ II B	♀ III A	♀ III BC	♀ III D	Juvenile
Offshore								
82			1					
84			1					
91			1			1	1	
95			1				1	
104			1			1	1	
106			1			1	1	
108			2			1	1	
112			2				2	
118			1			1	1	
122			2				1	
124			1				1	
141							1	
148							2	
Onshore								
102	1	2	1			1		
115-2		2	1					
129-2	1	2	1		1	1		
142	1	1	1		1	1		
143		2	1	1			1	
143-2	1	2	1			1	1	1
144	1	1	1	1	1	2		1
Total	5	12	21	2	3	11	18	2

Results

The integrated mean chlorophyll-*a* concentration in the upper 100 m was high at onshore stations and low at offshore ones (Figure 2). These data are cited from the cruise report of the 6th Antarctic Expedition by the R/V Kaiyo Maru (Fisheries Agency 1993). Composition of microplankton in the surface water at the stations where the foregut contents of *E. superba* were examined was mostly represented by three categories: *Nitzschia*, *Thalassiosira* and microzooplankton including naked ciliates and tintinnids. The relative abundances of the three plankton categories at each station shows that *Thalassiosira* were more numerous at onshore stations than at offshore ones. No distinct difference was found in *Nitzschia* and microzooplankton between the onshore and offshore stations (Figure 3).

The microplankton species found in the foregut contents of *E. superba* are outlaid in Table 2. At most stations the foregut contents of *E. superba* were dominated by diatoms, especially *Nitzschia* (*N. curta* and *N. kerguelensis*) and *Thalassiosira*. The exception was when *Rhizosolenia* were predominant in *E. superba* foreguts at Sts. 82 and 84.

Percent frequencies of the occurrence of the two diatom genera and of microzooplankton (mainly tintinnids) found in the foregut of *E. superba* of both onshore and offshore station groups are shown in Figure 4. *Nitzschia* were found the most frequently among the different prey categories in *E. superba* foreguts and were more frequently ingested in offshore individuals than onshore ones (Figure

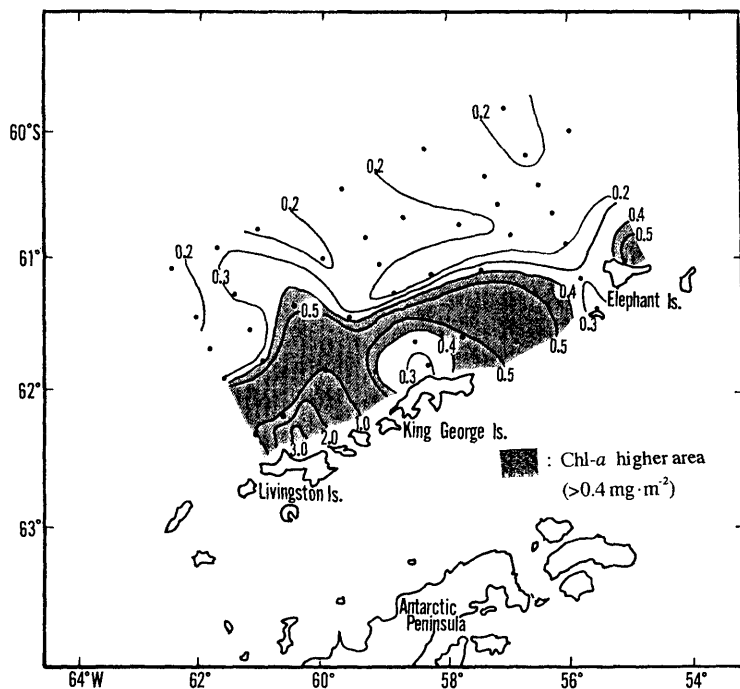


Fig. 2. Horizontal distribution of mean chl-*a* concentration integrated in the upper 100 m of the water column in Leg II. (After Fisheries Agency 1993)

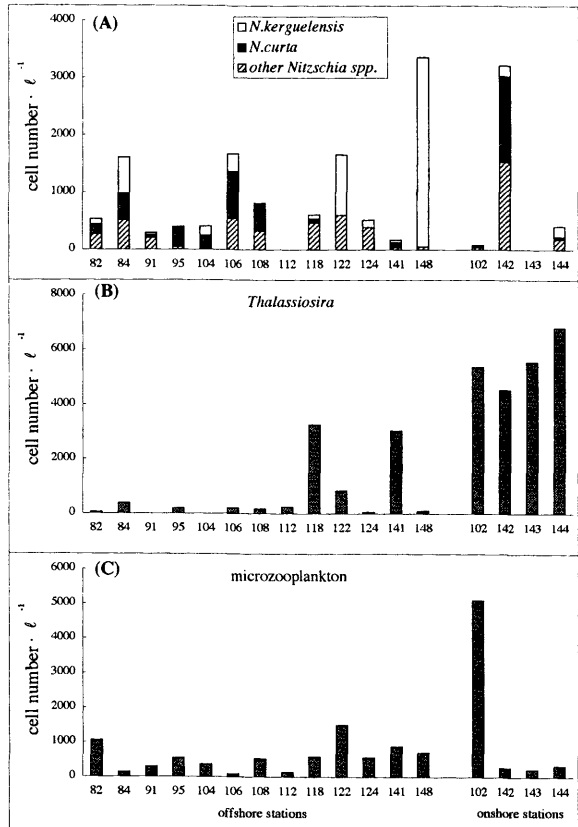


Fig. 3. Total density of (A) *Nitzschia*, (B) *Thalassiosira* and (C) microzooplankton (naked ciliates and tintinnids) in the surface water.

4A). This tendency was more marked in the case of *N. curta* and *N. kerguelensis* which were ingested at most stations (Figure 4A). *Thalassiosira* on the other hand were found more frequently in the foregut of onshore *E. superba* than the offshore ones (Figure 4B). Microzooplankton (mainly tintinnids) were more frequently ingested by onshore krill than by offshore ones (Figure 4C). The environmental food condition for *E. superba* in onshore waters seems to be superior as the high chlorophyll-*a* concentrations suggest. In contrast to diatoms, microzooplankton were more frequently ingested by the onshore krill than offshore ones.

The stages of sexual maturity in *E. superba* examined in this study are shown in Figure 5. The younger stages (juvenile; ♂: II A, III A; ♀: II B, III A) were dominant at the onshore stations whereas advanced stages (♂: III B; ♀: III BC, III D, III E) were more abundant at offshore stations. The younger stages occupied about 65% of total individuals examined (1492 individuals) by individual number at onshore stations, while advanced stages comprised 92% of a total of 1673 individuals at offshore stations.

At onshore stations the younger stages had ingested microzooplankton more frequently than the advanced stages. And the advanced stages of krill at offshore and onshore stations showed similar feeding preferences (Table 3).

The frequency of *E. superba* that ingested microzooplankton was the same at

Table 2. Items in the foregut content of *E. superba* identified in this study.

DIATOM		
Centrales		
<i>Asteromphalus hookeri</i>	<i>Asteromphalus hyalinus</i>	<i>Corethron criophilum</i>
<i>Coscinodiscus</i> spp.	<i>Dactyliosolen</i> sp.	<i>Guinardia</i> sp.
<i>Odontella</i> sp.	<i>Rhizosolenia alata</i>	<i>Rhizosolenia curvata</i>
<i>Rhizolenia setigera</i>	<i>Rhizosolenia simplex</i>	<i>Rhizosolenia styliiformis</i>
<i>Rhizosolenia</i> sp.	<i>Thalassiosira antarctica</i>	<i>Thalassiosira gracilis</i>
<i>Thalassiosira</i> sp.	<i>Tropidoneis antarctica</i>	
Pennales		
<i>Cocconeis</i> spp.	<i>Grammatophora arcuata</i>	<i>Licmophora gracillis</i>
<i>Licmophora</i> sp.	<i>Nitzschia directa</i>	<i>Navicula imperfecta</i>
<i>Navicula</i> sp.	<i>Nitzschia angulata</i>	<i>Nitzschia barbieri</i>
<i>Nitzschia clasterium</i>	<i>Nitzschia curta</i>	<i>Nitzschia cylindrus</i>
<i>Nitzschia heimii</i>	<i>Nitzschia kerguelensis</i>	<i>Nitzschia leointei</i>
<i>Nitzschia lineata</i>	<i>Nitzschia obliquecostata</i>	<i>Nitzschia pseudonana</i>
<i>Nitzschia ritscheri</i>	<i>Nitzschia separanda</i>	<i>Nitzschia sublineata</i>
<i>Nitzschia vanheurckii</i>	<i>Pleurosigma directum</i>	<i>Stauroneis charcotii</i>
<i>Thalassiothrix antarctica</i>	<i>Thalassiothrix longissima</i>	<i>Thalassiothrix</i> sp.
DINOFLLAGELLATES		
<i>Amphidinium</i> sp.	<i>Ceratium</i> sp.	<i>Dinophysis</i> sp.
<i>Gymnodinium</i> sp.		
SILICOFLAGELLATES		
<i>Distephauns speculum</i>		
FORAMINIFERA		
<i>Globigerina bulloides</i>		
TINTINNIDS		
<i>Cadonellopsis</i> sp.	<i>Cymatocilis brevicaudata</i>	
Unidentified species		
NAKED CILIATE		
Unidentified species		

both onshore and offshore stations for advanced stages (Table 4). There were significant differences between the microzooplankton ingested by the advanced and younger stages of *E. superba* ingested microzooplankton at onshore stations (Chi-square test for independence; $p < 0.01$, $\chi^2 = 7.8$, df: 1).

Discussion

The foregut contents of *E. superba* have been studied mainly based on samples collected in the summer season. Although some differences in the composition of the foregut contents of *E. superba* have been reported, the greater part of gut contents is composed of diatoms (Nemoto 1968, Ligowski 1982, Marchant & Nash 1986). Phytoplankton standing crops usually become high in summer, and *E. superba* have been considered to be a herbivorous animal of great importance as primary consumers throughout all of the Antarctic marine ecosystem (Barkley 1940, Nemoto 1968, Mauchline & Fisher 1969, Mauchline 1980, Kawamura 1981, Miller & Hampton 1989, El-Sayed 1990). Of the diatoms eaten by *E. superba*, small species

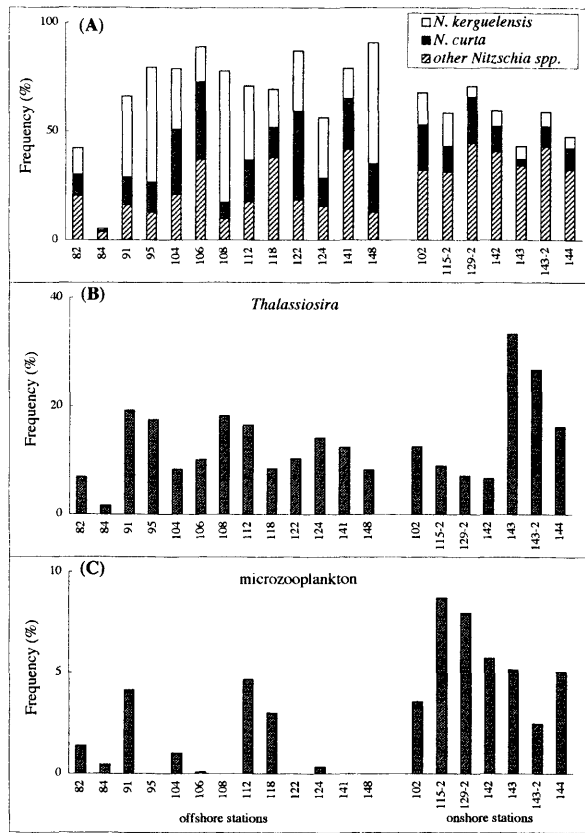


Fig. 4. Percent frequencies of occurrence of (A) *Nitzschia*, (B) *Thalassiosira* and (C) microzooplankton (mainly tintinnids) in the foregut of *E. superba*.

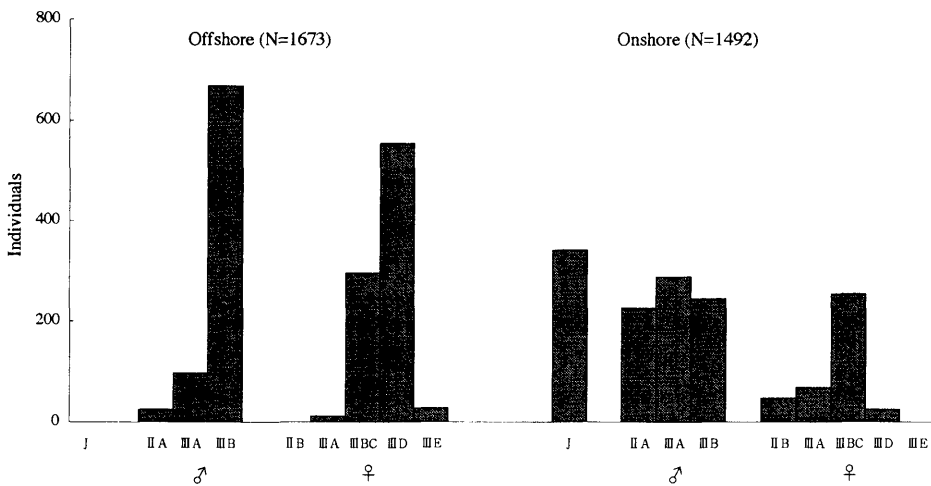


Fig. 5. Number of individuals of each sexual maturity stage of *E. superba* at the onshore and offshore station groups where the foregut contents were examined.

Table 3. Average percentage of N (*Nitzschia*) and M (microzooplankton) in the foregut contents of *E. superba* at offshore and onshore stations. Bars in the table indicate no occurrence.

	offshore N : M	onshore N : M
♂ III B	70.1 : 1.0 (n=14)	75.8 : 2.4 (n=7)
♀ III B C	79.4 : 0.6 (n=6)	74.4 : 4.2 (n=5)
♀ III D	67.6 : 1.8 (n=16)	84.7 : 0.0 (n=2)
♂ II A	—	37.5 : 5.4 (n=5)
♀ II B	—	50.0 : 9.4 (n=12)
♂ III A	—	52.9 : 6.5 (n=3)
♀ III A	—	50.6 : 12.0 (n=3)
Juvenile	—	73.8 : 4.6 (n=2)

such as *Nitzschia* spp. predominated over the survey area.

Euphausia superba are considered to undertake selective feeding (Barkley 1940, Nemoto 1968). From a comparison of the distributions of *E. superba* and phytoplankton, Kawamura (1981) suggested that *E. superba* ingested certain diatom species (*Nitzschia kerguelensis*, *Coscinodiscus* sp., *Synedra satula* and *Actinocyclus* sp.) selectively. On the other hand Pavlov (1971, 1974) and Meyer & El-Sayed (1983) are of the opinion that the foregut contents of *E. superba* are comprised of the small diatoms in many cases because the frustule of small species is strong and resists digestion but large diatoms such as *Rhizosolenia* and *Chaetoceros* have feeble frustules and are therefore scarce in foregut contents. In this study, small diatoms were generally predominant in the foregut contents, but in two cases (Sts. 82 and 84) the large diatom *Rhizosolenia* spp. occupied a large part of the foregut contents. While *Chaetoceros* spp. occurred in the surface water samples, no evidence of grazing on this diatom was found in the foregut contents of *E. superba*. This agrees with the hypothesis that *E. superba* avoid feeding on species with long terminal setae like *Chaetoceros* (Barkley 1940, Marr 1962, Naumov 1962, Nemoto 1968, Mauchline & Fisher 1969, Kawamura 1981). We therefore conclude that *E. superba* filter small diatoms selectively and do not ingest *Chaetoceros* spp.

A clear difference in the composition of the foregut contents of *E. superba* between onshore and offshore stations was found. At most offshore stations the greater part of the foregut contents was occupied by *Nitzschia*. At onshore stations on the other hand, a larger number of microzooplankton (mostly tintinnids) were

Table 4. No. of individuals of *E. superba* that ingested microzooplankton at the offshore and onshore station groups.

	Feeding	Non-Feeding
Offshore		
Advanced Stages	14 (40%)	21 (60%)
Onshore		
Advanced Stages	6 (40%)	9 (60%)
Younger Stages	4 (83.3%)	20 (16.7%)

found in the foregut contents of *E. superba* than at offshore stations. No significant difference was found in the density of *Nitzschia* or microzooplankton in the surface waters of the onshore and offshore stations. Although no data on the composition of microplankton at other depths is available in this study we assumed that the species assemblage of microplankton at the surface paralleled that at the water column because Hasle (1969) found that the difference in phytoplankton composition over sea area was larger than that of the vertical distribution and that the occurrence of the phytoplankton maxima was frequently found in the upper 10 m in the Antarctic Ocean. The sexual maturity stages of the specimens at onshore stations were lower than that of the offshore ones regardless of sex. In this context it is suggested that *E. superba* may switch prey items as sexual maturity proceeds. Concretely, the younger stages of krill have omnivorous habits, while the advanced stages are herbivorous. Indeed the younger stages had ingested microzooplankton more frequently than the advanced stages. The data from the feeding experiment by Schnack (1985) suggested that *E. superba* ingested *Nitzschia* selectively as body length increased but she did not refer to this point in her paper. Though the sexual maturity stages of *E. superba* used in her experiment are unknown, we assume that her data support our results.

Microzooplankton found in the foregut contents were mainly represented by tintinnids, which have lorica. In the surface seawater samples however, naked ciliates were found far more frequently than tintinnids. At St. 102 the density of naked ciliates was as high as diatoms in the surface seawater. This suggests that the importance of microzooplankton as a food of *E. superba* might be underestimated. Microzooplankton are probably as important a food item as diatoms.

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