INTRODUCTION

Patterns of prey selection by fish are the results of both predator and prey characteristics. The mechanisms responsible for prey selection by plankton-feeding fish have been examined in detail, but few studies of benthos-feeding fish have been reported. As most benthos exhibit some form of cryptic behavior, the detection of such prey is one of the most important processes in prey selection by benthic feeders. Among prey characteristics, the microhabitat (i.e. epifaunal, infaunal, etc.) of the benthos can play a significant role in prey detection by influencing the extent to which prey is exposed. For example, negative selection of infaunal species by benthic fish has been demonstrated. Once they have emerged from the bottom sediment, however, such species are heavily consumed. Prey size is also a major determinant in prey detection because reaction distances for fish increase with prey size. In addition, even after prey have been detected, the microhabitat and the size of prey may play important roles in prey selection by influencing difficulties in handling.

Red sea bream Pagrus major is one of the most important demersal fishes for coastal fisheries in Japan. This species is commonly distributed in seas around Japan, and the nursery grounds for their young are found on sandy bottoms at a depth of about 10 m. In Shijiki Bay, young red sea bream are densely distributed over the sandy bottoms of the inner part of the bay (about 10 m in depth) from June to September. Within this habitat, they feed mainly on gammaridean amphipods and grow from 25 mm fork length (FL) to 120 mm FL. When the consumed gammarids were identified at the species level, we observed dietary shifts as the young red sea bream increased in size. These shifts did not, however, correspond to changes in the species composition of gammarids in the environment. As the microhabitat and body size range of
gammarids differ among species, both factors might be expected to be closely related to the selection of gammarid species by young red sea bream.

The purpose of the present study was to examine the mechanisms responsible for prey selection by young red sea bream. By comparing the species composition of gammarids in the diet of red sea bream with that in the environment, we attempted to explain the pattern of prey selection. The results indicate that both the microhabitat and the body size of gammarids play important roles in prey selection by young red sea bream.

**MATERIALS AND METHODS**

**Sampling**

Sampling was performed during the daytime in Shijiki Bay (33°11'N, 129°24'E), Nagasaki Prefecture, western Japan, at 1- to 5-week intervals from June to October in 1982 and 1983, and from June to September in 1985. Fish and macrobenthos were collected from three sites (one main site and two additional sites) in the inner part of the bay (see Sudo and Azeta). The inner part of the bay consists of three areas with different substrata defined as the sandy bottom, the rocky bottom, and the eelgrass *Zostera marina* bottom. The study sites were located on the sandy bottom (water depth, approximately 10 m). The sediment consisted of well-sorted fine sand (median diameter, 0.177 mm) with silt and clay fractions accounting for less than 10% of the total; the organic content (weight loss after heating at 500°C for 5 h) was less than 6%.27

Fish were captured with a Gochi trawl23 once at each site on each sampling date. Two to 10 replicate collections were made at the main site for macrobenthos with a 0.05 m² Smith–McIntyre grab. All captured fish were preserved in 10% formalin. Samples of the macrobenthos retained on a 0.50 mm mesh sieve were preserved in 5% buffered formalin.

**Analysis of samples**

Twenty red sea bream that were collected from the main site on each sampling date were examined for dietary analysis. If less than 20 fish were available, fish from additional sites were also examined. The total number of fish examined was 202 in 1982, 167 in 1983, and 88 in 1985. The mean FL of the fish increased from 37.8 ± 4.0 mm (±SD) in June to 106.5 ± 12.2 mm in October 1982; from 32.3 ± 4.8 mm in June to 108.8 ± 12.6 mm in October 1983; and from 41.2 ± 3.8 mm in June to 108.3 ± 12.9 mm in September 1985. The contents of fish stomachs and macrobenthos were sorted, identified and quantified under a binocular microscope that was equipped with an ocular micrometer. Because gammarids were the most important prey item, we identified them at the species level and measured their body lengths (from the rostrum to the tip of the telson).

We classified gammarids into four types in terms of microhabitat: (i) epifauna, species living on or above the bottom surface (including free-living and tube-dwelling species); (ii) shallow burrowers, species that burrow into the superficial bottom sediment with the dorsal part of the body exposed above the surface of the bottom sediment; (iii) infaunal tube dwellers, species living in a tube inserted into the bottom sediment; and (iv) deep burrowers, species that dig deep into the bottom sediment. The classification was based on reports in the literature.928-36 Each item in every fish stomach was then dried at 110°C and weighed after a constant weight had been achieved.

**Analysis of data**

The contribution of each prey item to the diet was determined by a modified version of the calculation of the index of relative importance (IRI).37 The IRI was calculated as follows:

\[ IRI = (%N + %W)\%F \]

where %N is the numerical percentage of a given prey relative to the total diet; %W is its gravimetric percentage; and %F is the frequency of occurrence as a percentage of the total number of stomachs examined.

To quantify the similarity in species composition between gammarids in the diet and gammarids in the environment, we calculated a similarity index (SI) by using Schoener's Index as follows:

\[ SI = 1 - 0.5 \sum |p_{di} - p_{ei}| \]

where \( p_{di} \) and \( p_{ei} \) are the proportions by number of gammarid species \( i \) in the diet and in the environment, respectively. This index ranges from 0 (no similarity) to 1 (complete similarity).

Schoener's index was also used to estimate the degree of overlap in size between the two groups of gammarids; namely, those in the diet and those in the environment. Estimates were made by comparing size frequency distributions of the two groups of gammarids, which were divided into body length classes at 1 mm intervals. To calculate
the overlap index (OI), \( pd_i \) and \( pe_i \) in Eqn 2 were taken as the proportions by number of gammarids in size class \( i \) in the diet and in the environment, respectively.

Selectivity by fish for gammarids in terms of their microhabitat was calculated for individuals by using Manly's \( \alpha_{ij} \). The selectivity, \( \alpha_i \), was calculated as follows:

\[
\alpha_i = \frac{r_i/n_i}{\Sigma r_i/n_i}, \quad i = 1, \ldots, m
\]

where \( r_i \) and \( n_i \) are the proportions by number of gammarids in microhabitat type \( i \) in the diet and in the environment, respectively. This index ranges from 0 (complete avoidance) to 1 (complete preference). When \( \alpha = 1/m \), a given prey is consumed in proportion to its availability (neutral preference). Because we categorized gammarids into four types in terms of microhabitat, the value of \( \alpha \) that represents neutral preference is 0.25.

**RESULTS**

**Species composition of gammarids**

In terms of gross taxonomic composition, the diet of young red sea bream did not vary among the 3 years during which measurements were made (Fig. 1). Gammaridean amphipods contributed from 53% to 98% of the total IRI between June and September and were, by far, the most important source of food. Fish eggs and mysids were also important, although both items accounted for less than 30% of the total diet. In October, when young red sea bream began to expand their habitat, the contribution of gammarids to their diet decreased, whereas that of polychaetes and fish, which are larger prey items, increased.

In the identification of gammarids at the species level, we found 45 species (23 families, 31 genera) and 61 species (23 families, 40 genera) in the stomachs of the fish and in the sediment, respectively (Table 1). The species composition of gammarids found in the fish stomachs varied between months (Fig. 2). Various species, such as *Byblis japonicus*, *Aoroides* sp., *Protomedea crudoliops*, *Paradexamine marlie*, *Abludomelita denticulata*, *Synchelidium lenorostrale*, and *Tiron ovatibasis* were frequently consumed between June and mid-July, although individual species never accounted for more than 50% (by number) of the gammarids in the diet. After mid-July, however, *B. japonicus* accounted for the great majority of consumed gammarids: from 35% to 81% in 1982; from 82% to 100% in 1983; and from 60% to 83% in 1985. *Ampelisca bocki*, *Ampelisca brevicornis*, and *Ampelisca miharaensis*, which belong to the same family (Ampeliscidae) as *B. japonicus*, were also common species in the stomachs of the fish during these months. In contrast, common species collected from the sediment were *B. japonicus*, *A. bocki*, *P. crudoliops*, *Harpiniopsis vadiculus*, and *Urothoe* sp. C, but each species individually never exceeded 50% of the total gammarids at any sampling (Fig. 2).

Comparisons between the species composition of gammarids in the diet and that in the environment revealed that they were often dissimilar. In fact, the similarity indices (SI); that is, measurements of similarity in species composition between dietary and environmental gammarids, were low, ranging from 0.01 to 0.62 (mean \( \pm \) SD, 0.36 \( \pm \) 0.12). Thus, each gammarid species was not consumed as prey by red sea bream in proportion to their relative abundance in the environment.

**Microhabitats of gammarids**

The composition of gammarid species found in the stomachs of the fish varied in terms of
<table>
<thead>
<tr>
<th>Species</th>
<th>Stomach</th>
<th>Environment</th>
<th>Microhabitat</th>
<th>Species</th>
<th>Stomach</th>
<th>Environment</th>
<th>Microhabitat</th>
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<td><em>Ampelisca bocki</em></td>
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<td><em>Colomatia</em> sp.</td>
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<td>–</td>
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<td>IT</td>
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<td><em>Synopia ultramarina</em></td>
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<td><em>Abludomelita denticulata</em></td>
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<td>+++</td>
<td>EF</td>
<td><em>Tiron ovatibasis</em></td>
<td>+++</td>
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(*+++*) Species occurring in each of 3 years; (+++) in each of 2 years; (+) in 1 year; (–) absence.
EE, epifauna; SB, shallow burrowers; IT, infaunal tube dwellers; DB, deep burrowers.
Gammarids predated by P. major

**FISHERIES SCIENCE**

393

Fig. 2  Species composition (% by number) of gammarids in (left) the stomachs of young red sea bream and in (right) the sediment in: (a) 1982; (b) 1983; and (c) 1985. Bj, *Byblis japonicus*; Ao, *Ampelisca bocki*; Ar, *Ampelisca brevicornis*; Ah, *Ampelisca miharaensis*; Pc, *Protomedea crudoliops*; Ac, *Aoroides* sp.; Ad, *Abludomelita denticulata*; Sl, *Synchelidium lenorostratum*; Pm, *Paradexamine marlie*; To, *Tiron ovatibasis*; Hv, *Harpiniopsis vadicus*; Ub, *Urothoe* sp. C; Ot, *Bubcorophium tanabensis*; Ot, other gammarids.

Microhabitat type (see Table 1), with quite a similar pattern occurring during each of the 3 years but which changed markedly over the course of each sampling season (Fig. 3). Epifaunal and shallow-burrowing species accounted for the majority of gammarids consumed by young red sea bream before mid-July. After mid-July, however, the contribution of infaunal tube-dwelling species increased sharply and accounted for the great majority of gammarids consumed: from 77% to 90% (by number) in 1982; from 96% to 100% in 1983; and from 95% to 99% in 1985. Deep-burrowing species never accounted for more than 10% of the gammarids during any of the study periods. In contrast, in terms of microhabitat type, the composition of gammarids in the sediment was relatively constant during the study periods (Fig. 3). Infaunal tube-dwelling species were the most abundant type of gammarids in 1982 (mean ±SD, 55 ±8%), as well as in 1983 (51 ±11%) and 1985 (39 ±13%). Deep-burrowing species were also abundant (approximately 30% of the gammarids in each year). Epifaunal or shallow-burrowing species were the least abundant types.

In terms of microhabitat type, the patterns of selectivity for gammarids by young red sea bream were similar among the 3 years (Fig. 4). Epifaunal species were selectively consumed before mid-July but were subsequently avoided. Shallow-burrowing species were consumed approximately in proportion to their abundance in the environment before mid-July but were clearly avoided thereafter. By contrast, infaunal tube-dwelling species were not selected before mid-July but were strongly selected thereafter. Deep-burrowing species were almost completely avoided during all these study periods. In terms of microhabitat type, these distinct patterns of selectivity for gammarids suggest that microhabitat plays an important role in prey selection by young red sea bream.
Body size of gammarids

As the body size of the fish increased between June and August, the mean body length of the gammarids consumed by the young red sea bream increased from approximately 2–7 mm (Fig. 5). The increase in gammarids’ size was slow from June to mid-July but was rapid thereafter. The length of gammarids then remained approximately constant, although the red sea bream continued to grow in size.

We analyzed the body lengths of 14 abundant species of gammarids in the environment in June and August because there was a remarkable difference between patterns of gammarid selection by young red sea bream before and after mid-July (Figs 2,4). In June, epifaunal species, such as Paradexamine marlie, Tiron ovatibasis, Abludomelita denticulata and Aoroides sp., had a mean body length of approximately 2–3 mm; a shallow-burrowing species, Synchelidium lenorostralum, was about 2–4 mm long; infaunal tube-dwelling species such as Ampelisca naikaiensis, Ampelisca miharaensis, Ampelisca bocki, and Byblis japonicus were about 2–5 mm long, although Protomedeia crudoliops was only about 2–3 mm long; and deep-burrowing species such as Harpiniopsis miharaensis, Harpiniopsis vadiculus, Urothoe sp. B and Urothoe sp. C were about 2–3 mm long (Fig. 6). Among the 14 species, four ampeliscid species (three species of Ampelisca and B. japonicus) exhibited the largest standard deviation and range of body lengths. In August, the mean body lengths of epifaunal species, shallow-burrowing species, deep-burrowing species, and one of the infaunal tube-dwelling species, P. crudoliops, were about 2–3 mm (Fig. 6). The mean body lengths of four ampeliscid species were about 3–5 mm. The means, standard deviations and ranges in body length of these four species were larger than the others.

We compared the body lengths of the 14 gammarid species collected from the sediment with those of all gammarids found in the stomachs of
the red sea bream. In June, body lengths of most species in the sediment were similar to those of all gammarids in the stomachs (the mean was approximately 2–3 mm; Fig. 6). In fact, the overlap index (OI), which is a measure of the size distribution overlap between gammarids in the sediment and those in the stomach of fish, exceeded 0.5 for almost every species (Table 2). Thus, the gammarid species in the sediment appeared to be suitable prey for young red sea bream in terms of body size. However, the heavily consumed gammarids were almost exclusively the epifaunal and shallow-burrowing species. In spite of its numerical dominance in the sediment, _B. japonicus_, an infaunal tube-dwelling species, was consumed in only small numbers. Furthermore, deep-burrowing species were hardly consumed (Figs 2,3). Accordingly, the body size of prey could not, by itself, account for the pattern of selection of gammarid species by young red sea bream in June. In August, when body lengths of gammarids in the stomachs were larger (the mean body length was approximately 6–7 mm), the mean body length of each gammarid species in the environment was smaller than the mean body length of the ingested gammarids (Fig. 6). Only two infaunal tube-dwelling species, _A. bocki_ and _B. japonicus_, gave values of OI greater than 0.5 (Table 2) because both amphiliscids were the largest species of gammarids in the environment. Epifaunal and deep-burrowing species, in particular, gave the lowest OI values, which were less than 0.2. This indicates that these species were apparently too small to serve as prey for young red sea bream. Thus, the pattern of selection of gammarid species in August could be explained by prey body size.

**DISCUSSION**

**Significance of prey microhabitat**

By influencing the processes of detection and handling of prey, the microhabitat of prey (i.e. epifaunal, infaunal, etc.) can play an important role in prey selection by benthic feeders. An earlier study of young red sea bream demonstrated that epifaunal prey were most commonly selected by these fish. Similar results have been obtained for other fish species. Data obtained in the present study also indicated the importance of the prey's microhabitat because we observed distinct differences in patterns of selectivity for gammarids by young red sea bream in terms of microhabitat type (Fig. 4).

Before mid-July, the order of selectivity for gammarids with four types of microhabitat was epifaunal species > shallow-burrowing species > infaunal tube-dwelling species > deep-burrowing species.
also influence the difficulty in the capture and manipulation of prey because the fish must extract infaunal species and separate them from sediment or a tube (we seldom found any sediment or tubes in the stomachs of the fish). Hence, the vertical distribution of gammarids in the sediment can influence the duration of their handling by young red sea bream. Because the handling time can be expected to increase with increased burial depth, differences in handling difficulty among gammarids should also contribute to differences in selectivity.

We classified gammarid species into four groups in terms of their microhabitats. However, a prey species does not always have a uniform microhabitat. For example, many infaunal species exhibit diel vertical migration for their essential activities.
such as dispersal, feeding, and mating.\textsuperscript{10,12,44–48} These vertical movements result in changes in microhabitat and, hence, they affect susceptibility to predation. In fact, as published elsewhere, the predation of \textit{Byblis japonicus}, which is the most abundant species in the sediment, by young red sea bream in June is limited during the day, which is when these gammarids are in their tubes. However, once juvenile \textit{B. japonicus} emerge for dispersal at night,\textsuperscript{9,12} these individuals are subject to heavy predation at dusk and dawn\textsuperscript{9} (young red sea bream cease to feed after dark). Similarly, mature males of \textit{B. japonicus} are preyed upon exclusively by nocturnal barface cardinalfish \textit{Apogon semilineatus} when they enter the water column to make mating contact at night.\textsuperscript{12} These diel changes in the intensity of predation on \textit{B. japonicus} correspond to changes in the microhabitat and strongly support the proposed importance of prey microhabitat in prey selection by benthic feeders.

### Significance of prey size

Although prey microhabitat is undoubtedly a major determinant in prey selection, the microhabitat of gammarids is, by itself, insufficient when accounting for prey selection by young red sea bream because epifaunal species were avoided and infaunal tube-dwelling species were strongly selected after mid-July (Fig. 4). When we examined them on the basis of body size, however, we found that epifaunal, shallow-burrowing and deep-burrowing species in the environment were much smaller than ingested gammarids in August (Fig. 6; Table 2). Although infaunal tube-dwelling \textit{Byblis japonicus} was also smaller than the ingested gammarids, it had the largest body length and, hence, it gave the greatest overlap with ingested gammarids in terms of size distribution. Accordingly, the fact that the body size of \textit{B. japonicus} is largest seems to be responsible for the almost exclusive predation on this species as young red sea bream require large prey. By contrast, because epifaunal, shallow-burrowing, and deep-burrowing species were too small to feed on, these species were excluded from the diet of the red sea bream after mid-July. It has been demonstrated that predatory fish prefer relatively larger prey as they themselves increase in size,\textsuperscript{19,49–52} as was the case for young red sea bream (Fig. 5). Therefore, the shift to larger prey with the growth of the fish would be expected to result in changes in the type of species of gammarids ingested and in the almost exclusive predation of \textit{B. japonicus} after mid-July.

As mentioned earlier, epifaunal and shallow-burrowing gammarids are more easily detected because of their high degree of exposure. However, the selectivity for these gammarids by young red sea bream was low after mid-July (Fig. 4). Because there is a positive correlation between prey size and reaction distance for fish,\textsuperscript{1,13–15,17,18} the relatively smaller body size should decrease the reaction distance between the gammarids and the fish. Accordingly, it seems most likely that the reduction in their detectability due to their smaller body size outweighed the high detectability due to their

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### Table 2  Overlap in size distribution between individual gammarid species in the environment and all gammarids in the stomachs as quantified by Schoener’s Index*  

<table>
<thead>
<tr>
<th>Species†</th>
<th>June</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pm</td>
<td>0.573</td>
<td>0.378</td>
</tr>
<tr>
<td>To</td>
<td>0.896</td>
<td>0.389</td>
</tr>
<tr>
<td>Ad</td>
<td>0.836</td>
<td>0.554</td>
</tr>
<tr>
<td>Ac</td>
<td>0.201</td>
<td>0.581</td>
</tr>
<tr>
<td>Sl</td>
<td>0.856</td>
<td>0.736</td>
</tr>
<tr>
<td>Pc</td>
<td>0.540</td>
<td>0.628</td>
</tr>
<tr>
<td>An</td>
<td>0.574</td>
<td>0.431</td>
</tr>
<tr>
<td>Ao</td>
<td>0.430</td>
<td>0.510</td>
</tr>
<tr>
<td>Bj</td>
<td>0.487</td>
<td>0.814</td>
</tr>
<tr>
<td>Hm</td>
<td>0.579</td>
<td>0.573</td>
</tr>
<tr>
<td>Hv</td>
<td>0.840</td>
<td>0.618</td>
</tr>
<tr>
<td>Ub</td>
<td>0.902</td>
<td>0.365</td>
</tr>
<tr>
<td>Uc</td>
<td>0.927</td>
<td>0.817</td>
</tr>
</tbody>
</table>

* Overlap values greater than 0.5 are in boldface.
† Abbreviations representing names of species of gammarids are explained in the legend to Fig. 6.
exposure with consequently low selectivity for epifaunal and shallow-burrowing species after mid-July. Higher cost to benefit ratios associated with eating these smaller gammarids might also be responsible for their low selectivity. When considering deep-burrowing gammarids, both their deepest burial depth and their small body size undoubtedly contributed to the almost total exclusion of these gammarids from the diet of young red sea bream.

There is no doubt that because the infaunal tube-dwelling species \textit{B. japonicus} has the largest body size, this contributes to its high selectivity after mid-July as young red sea bream require large prey. However, it is unclear as to how young red sea bream are able to feed efficiently on infaunal tube-dwelling \textit{B. japonicus}, which would not be easily detected and handled. During the day, \textit{B. japonicus}, as well as other ampeliscid species, live in a tube that extends downwards a few centimeters into the sediment. However, the tube has an opening at its upper end which is as much as 1 cm above the bottom surface.\textsuperscript{28,53} Therefore, young red sea bream may be able to detect the wide opening of the tube (larger individuals have larger tubes with a wider opening) rather more easily than smaller epifaunal and shallow-burrowing gammarids. Schmitt and Holbrook\textsuperscript{54} stated that adult black surfperch preferred more tubicolous gammarids than did juveniles because of the ontogenetic development of their winnowing behavior. However, a shift in foraging behavior is unlikely to occur in red sea bream because, as indicated by underwater observations, larger fish appear to feed by using visual picking behavior as do smaller fish.

A more likely explanation for the high selectivity for \textit{B. japonicus} is an increase in the ability of the fish to handle prey as the fish grow larger. The development of mouth morphology with increasing fish size, increases in the size and protrusion of the mouth, increases in the volume of the buccal cavity, and changes in the associated jaw structure might enable young red sea bream to extract a tube that contains \textit{B. japonicus} from the sediment and separate the body from the tube. In fact, no die changes have been observed in the intensity of predation on this gammarid in August (H Sudo, unpubl. data, 2000), suggesting that, irrespective of whether \textit{B. japonicus} is in a tube or not, the difficulty in handling is similar for the larger fish. The slower increase in size of ingested gammarids between June and mid-July (Fig 5), which is when young red sea bream do not have such developed handling skills, is probably due to the low level of large epifaunal and shallow-burrowing species in the environment. Similarly, in spite of a requirement for larger prey in October, the fish might be unable to find sufficiently large gammarids in the environment. This issue might explain, in part, why young red sea bream shift their diet from gammarids to polychaetes or fish and have to expand their habitat.

Both the microhabitat and the size of prey appear to determine prey selection by young red sea bream. Before mid-July, abundant gammarid species in the environment were the prey most suitable for the fish in terms of body size but not in terms of microhabitat. After mid-July, by contrast, most species were suitable prey in terms of microhabitat but not in terms of body size. This finding indicates that the prey’s microhabitat limited the diet of young red sea bream before mid-July, whereas prey size was the limiting factor thereafter. The significance of prey size in prey selection by planktivorous fish has been well documented.\textsuperscript{2,15–20,55} Because the role of prey size in prey selection is thought to be similar in planktivorous and benthos-feeding fish, size is probably one of the most important factors that determine prey selection by benthos-feeding fish. However, few studies have examined the role of prey microhabitat in prey selection by such fish.\textsuperscript{8,9,12,35} More attention should be paid to the microhabitat of prey because benthic prey have varied microhabitats. We have shown here that microhabitat influences both the detection and handling of prey via changes in the extent of the prey’s exposure and accessibility and in the difficulty of capturing and manipulating prey. Thus, it seems clear that the prey’s microhabitat plays a significant role in prey selection by benthos-feeding fish.

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