

# Differences in food composition between territorial and aggregative juvenile crimson sea bream *Evynnis japonica*

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**ABSTRACT:** Food composition, fork length and condition factor of juvenile crimson sea bream *Evynnis japonica* were examined for two behaviorally distinct types of fish inhabiting a nursery ground. Studies were carried out from March to September 1996 at Morode Cove, Ehime Prefecture, Japan. One type of fish is solitary and territorial and the other type is aggregative. The food compositions of the two types of fish were different. Solitary fish foraged mainly on Gammaridea and Caprellidea (benthic organisms), and Copepoda (planktonic organisms); while aggregative fish foraged mainly on Copepoda, Appendiculata and Cladocera (planktonic organisms). These findings suggest that when we study food composition of *E. japonica*, it is imperative to consider whether the samples used for the analyses are from solitary (territorial) fish. Solitary fish showed significantly greater fork length and condition factor than aggregative fish, suggesting that the former will have a greater fitness value than the latter.

**KEY WORDS:** behavior, crimson sea bream, food composition, intraspecific difference, juvenile.

## INTRODUCTION

Intraspecific food segregation in relation to dominance hierarchy has been mainly studied in freshwater fish.<sup>1–4</sup> However, clear food segregation with regard to the intraspecific social relationships in marine fish has not been studied.

Crimson sea bream *Evynnis japonica* and the closely related red sea bream *Pagrus major* are both economically important species from the coastal waters of Japan.<sup>5</sup> Since juveniles of *E. japonica* and *P. major* both utilize the sandy substrate of the sea as a habitat,<sup>6</sup> the interspecific trophic relationships between the two species are considered to be very competitive.<sup>7–9</sup>

In recent years, Kudoh and Yamaoka studied the ecological factors that influence juvenile *E. japon-*

*ica*.<sup>10,11</sup> Their studies demonstrated that the juveniles are composed of two behaviorally distinct types: a solitary type showing territoriality and an aggregative type, as in the case of *P. major*.<sup>10–15</sup> Juvenile crimson sea bream belonging to the two types shared the same sandy substrate habitat at the same site as the present study. This suggests that there is a carrying capacity for individuals of the solitary type.<sup>10,11</sup>

Although these studies showed that some differences could be found between the habitat selection and feeding behaviors of the two species, their stomach contents were not examined.<sup>10–15</sup> Furthermore, before 1990, all ecological studies on the interspecific feeding relationships between juveniles of the two species came from results of stomach content analyses of samples collected by fishing gear operated without discriminating between the behavioral types of the fish. Hence, the studies did not take into account the intraspecific behavioral differences in feeding. The aim of the present paper is to demonstrate the importance of testing for behavior-driven intraspecific food segregation, in order to understand the interspecific relationships between the two species. The present study might be the first in marine fish that deals with food composition, growth and

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**Table 1** Fork length in solitary and aggregative types of juvenile crimson sea bream

Month	Solitary		Aggregative		P-value*
	Fork length (mm)	No. fish	Fork length (mm)	No. fish	
May	62.4 ± 6.2 (55.1–77.7)	22	52.7 ± 3.3 (46.4–61.9)	25	P < 0.001
June	68.2 ± 9.7 (53.3–94.6)	19	55.3 ± 3.8 (48.8–60.3)	20	P < 0.001
July	75.5 ± 4.0 (68.8–83.8)	24	71.9 ± 4.7 (65.9–84.0)	17	P < 0.05
August	– –		75.0 ± 2.4 (72.2–79.5)	7	
September	80.9 ± 1.3 (80.0–81.8)	2	88.4 ± 4.2 (85.5–91.4)	2	

\*Significant differences were found by Mann–Whitney *U*-test between the two fish types – solitary and aggregative.

†The range is given in parentheses below the mean ± SD. Means are followed by SD.

condition factor in the context of a behavioral distinction.

## MATERIALS AND METHODS

Underwater observations of behavioral type and sample collection of juvenile *E. japonica* were undertaken from March to September 1996. Studies were carried out over a sandy substrate at a depth of approximately 8 m in a nursery at Morode Cove in Ehime Prefecture, Shikoku Island, Japan (33°00' N, 132°30' E).

At first, behavioral type was discriminated underwater to determine whether a fish was solitary or aggregative. According to Kudoh and Yamaoka, solitary fish are always territorial; therefore in the present study we regarded solitary fish as territorial.<sup>10</sup> Kudoh and Yamaoka determined whether a fish was territorial by observing the reactions of a given fish towards approaching conspecific or heterospecific species, both inside and outside a 50 cm radius.<sup>10</sup> Each fish was observed twice for 10 min each time. Fish were collected one by one with a small gill-net by scuba divers.

Fish were collected between 09:00 and 13:00 h. Solitary fish were collected on 14 May, 12 and 13 June, 1 and 5 August, and 21 September 1996. Aggregative fish were collected on 10 May, 12 June, 30 July, 22 August and 9 September 1996. Solitary fish collected on 1 and 5 August were treated as samples from July, due to the sample size and the close proximity to July. In most cases, samples of solitary and aggregative fish could not be collected on the same dates due to time constraints. After the collection, gut contents and whole fish were preserved by the injection of a 10% seawater formalin

solution into the body cavity and the immersion in the same solution, respectively. Fork length (FL) and numbers of each behavioral type examined in the present study are shown in Table 1.

Standard length, FL and body weight were measured for each sample. Condition factor (*K*) was calculated as:

$$K = \text{weight}/(\text{length})^3.^{16}$$

When measuring body weight, the formalin solution injected into the body cavity was removed as much as possible. Prey animals found in the stomach were taxonomically examined using a stereoscopic microscope to determine the level of class or suborder. Three methods, generally following Hynes' approach,<sup>17</sup> were used to analyze the stomach contents: the numerical method (the rate of individual numbers of a particular food item found in all guts examined); the points method (a type of volumetric method); and the occurrence method (the proportion of fish guts containing a particular food item). With the points method, if the stomach was full or extremely full, 24 and 32 points were awarded, respectively. If the amount of a prey category was smaller than 1 point, its quantitative evaluation was excluded from the results of the point method. The index of relative importance (IRI) was used for main prey items to combine the three measures, which allows the prey items to be ranked.<sup>18</sup> In the present study

$$\text{IRI} = (\%N + \%V) (\%F),$$

where *N* is the rate of individual numbers of a particular food item found in all guts examined, *V* is the value of the point method and *F* is that of the occurrence method.

## RESULTS

### Fork length

The FL of solitary fish was compared to that of aggregative fish (Table 1). The FL of solitary fish in May, June and July (when the sample size was sufficiently large for a comparison), was significantly larger than that of aggregative fish (Mann–Whitney *U*-test;  $P < 0.001$  in May and June,  $P < 0.05$  in July).

### Condition factor

In May and July solitary fish had significantly larger condition factor values than aggregative fish (Mann–Whitney *U*-test,  $P < 0.001$  in May,  $P < 0.01$  in July; Table 2). Although solitary fish showed a larger *K*-value than aggregative fish in June, this was not significant (Table 2).

### Stomach content analyses

#### Numerical method

Solitary fish of the 50 mm FL class (50.0–59.9 mm) mainly foraged on Copepoda, Appendicularia, and Gammaridea. Caprellidea was also a considerable food source (Table 3). When fish reached the 60 mm FL class, Copepoda content was high, but then decreased to 24.3% when the fish reached the 70 mm FL class. Intake of Gammaridea and Appendicularia increased in this size class. When fish reached the 80 mm FL class the intake of Gammaridea was the highest, followed by Copepoda, Caprellidea and Cumacea. In the 90 mm FL class the rate of Gammaridea intake was extremely high and Cirripedia larvae were also consumed (Table 3).

Aggregative fish in 40 and 50 mm FL size classes foraged mostly on Copepoda at a rate of 84.2% and

80.6%, respectively. Appendicularia was the next most common source of food for this size of fish (Table 3). Fish in the 60 mm FL size class decreased their rate of Copepoda intake to 20.9% but increased their intake of Appendicularia and Cladocera. At a size class of 70 mm FL, the rate of Cladocera intake increased and that of Copepoda decreased. Fish >80 mm FL showed a tendency to increase their intake of Copepoda and other planktonic organisms. These results indicate that fish of the aggregative type preyed mainly on planktonic organisms, such as, Copepoda, Appendicularia and Cladocera (Table 3).

In the 60 and 70 mm FL size classes, the aggregative fish fed primarily on Cladocera, but the solitary fish seldom consumed Cladocera (max = 3.7%). In contrast, the aggregative fish seldom consumed Gammaridea or Caprellidea (max = 4.5%), thus showing benthic habits, whereas the solitary fish used these species as their main source of food (max = 90.9%; Table 3).

#### Points method

Solitary fish in the 50–80 mm FL size classes foraged mainly on Gammaridea and Caprellidea (benthic animals) and these two types of prey comprised 49.8–62.5% of the total intake (Table 4). However, the rate of Gammaridea intake gradually decreased with growth. Fish in the 60 and 70 mm size classes consumed fish eggs at the rate of 13.0% and 15.9%, respectively, in addition to the Gammaridea and Caprellidea. Fish in the 80 mm size class mainly foraged on Caprellidea.

Aggregative fish in the 40 and 50 mm FL size classes foraged mostly on Copepoda. The second most preferred food source was Appendicularia (Table 4). The rate of Copepoda intake decreased gradually with growth. In the 60 mm and 70 mm FL size classes, the rate of Cladocera intake increased to a maximum of 42.3% and 59.8%, respectively. The intake of Appendicularia also increased (Table 4).

These findings show that solitary fish mainly foraged on Gammaridea and Caprellidea (benthic animals). Fish of the aggregative type consumed mainly zooplankton, such as, Copepoda, Appendicularia and Cladocera.

#### Occurrence method

Solitary fish in the 50 mm and 60 mm FL size classes foraged mainly on Gammaridea (Table 5). However, in the 70 mm and 80 mm size classes, the rates of intake decreased. High rates of

**Table 2** Condition factor ( $\times 1000$ ) of two behavioral types of juveniles†

Month	Solitary	Aggregative	<i>P</i> -value*
May	34.0 $\pm$ 1.9	30.7 $\pm$ 2.8	$P < 0.001$
June	35.5 $\pm$ 2.5	34.3 $\pm$ 1.7	NS
July	38.0 $\pm$ 3.3	34.5 $\pm$ 2.4	$P < 0.01$
August	–	38.5 $\pm$ 2.8	–
September	39.0 $\pm$ 1.0	35.9 $\pm$ 1.5	–

\*Significant differences were found by Mann–Whitney *U*-test between the two types, solitary and aggregative; NS, not significant. Means are followed by SD.

†The number of fish examined is as in Table 1.

**Table 3** Changes in food composition analyzed by the numerical method with growth

Fork length class (mm)	Solitary					Aggregative					
	50	60	70	80	90	40	50	60	70	80	90
Food items (%)											
Copepoda	32.7	75.8	25.3	19.1	–	84.2	80.6	20.9	8.8	45.5	33.3
Appendiculata											
Appendicularia	24.9	6.6	17.4	2.7	–	13.2	16.4	36.7	24.1	18.2	20.0
Nematoda	0.1	0.1	0.2	–	–	–	0.1	0.2	0.1	4.5	–
Branchiopoda											
Cladocera	–	0.1	3.7	–	–	0.1	0.1	39.5	64.1	9.1	–
Ostracoda	2.6	0.2	2.2	4.5	–	0.7	0.2	0.1	0.3	9.1	–
Cirripedia larvae	0.3	0.4	4.4	–	9.1	1.2	0.6	1.2	0.5	–	–
Malacostraca											
Amphipoda											
Gammaridea	21.3	7.6	25.5	26.4	90.9	0.1	0.8	0.3	0.3	4.5	–
Caprellidea	11.1	2.6	2.6	18.2	–	–	0.2	0.1	0.1	–	–
Cumacea	2.9	1.6	3.9	7.3	–	0.0	0.1	0.1	0.1	–	–
Tanaidacea	1.1	0.9	3.3	3.6	–	0.0	0.0	0.1	–	–	–
Isopoda	0.1	0.1	0.7	–	–	–	0.0	–	–	–	–
Mysidacea											
Mysida	0.1	–	0.7	3.6	–	–	0.0	–	–	–	20.0
Decapoda	0.1	0.3	2.0	4.6	–	0.0	0.3	0.5	1.0	9.1	13.3
Bivalvia	–	0.1	0.2	–	–	–	–	–	–	–	–
Gastropoda	–	0.1	1.5	3.6	–	–	–	–	–	–	–
Cephalopoda larvae	–	0.1	–	–	–	0.0	0.0	–	–	–	–
Ophiuroidea	0.1	–	–	–	–	–	0.2	–	0.5	–	–
Polychaeta	1.9	0.9	3.9	3.6	–	–	–	–	–	–	6.7
Fish eggs	0.4	2.8	2.4	1.8	–	0.3	0.3	0.4	0.3	–	–
Fish larvae	–	–	0.2	0.9	–	–	–	–	–	–	6.7
No. of fish examined	14	17	24	5	1	10	27	11	15	2	1

**Table 4** Changes in food composition analyzed by the points method with growth

Fork length class (mm)	Solitary					Aggregative				
	50	60	70	80	90	40	50	60	70	90
Food items (%)										
Copepoda	7.9	13.7	6.3	–	–	85.1	73.9	33.3	15.2	33.3
Appendiculata										
Appendicularia	2.4	2.5	3.2	–	–	14.9	24.7	24.4	25.0	–
Ostracoda	2.4	–	–	–	–	–	–	–	–	–
Branchiopoda										
Cladocera	–	–	–	–	–	–	–	42.3	59.8	–
Malacostraca										
Amphipoda										
Gammaridea	39.6	29.2	27.0	12.5	100.0	–	1.1	–	–	–
Caprellidea	40.2	25.5	23.8	50.0	–	–	–	–	–	–
Cumacea	1.2	6.8	1.6	–	–	–	0.4	–	–	–
Tanaidacea	–	0.6	1.6	–	–	–	–	–	–	–
Isopoda	–	–	3.2	–	–	–	–	–	–	–
Mysidacea										
Mysida	–	–	3.2	–	–	–	–	–	–	33.3
Decapoda	–	7.5	–	12.5	–	–	–	–	–	33.3
Bivalvia	–	–	1.6	–	–	–	–	–	–	–
Gastropoda	–	–	6.3	–	–	–	–	–	–	–
Polychaeta	2.4	1.2	–	–	–	–	–	–	–	–
Fish eggs	3.7	13.0	15.9	–	–	–	–	–	–	–
Fish larvae	–	–	6.3	25.0	–	–	–	–	–	–

The number of fish examined in each class is as in Table 3.

**Table 5** Changes in food composition analyzed by the occurrence method with growth

Fork length class (mm)	Solitary				Aggregative			
	50	60	70	80	40	50	60	70
Food items (%)								
Copepoda	100.0	94.1	83.3	80.0	100.0	100.0	100.0	86.7
Appendiculata								
Appendicularia	14.3	11.8	25.0	40.0	90.0	81.5	90.9	93.3
Nematoda	7.1	5.9	4.2	–	–	11.1	18.2	6.7
Branchiopoda								
Cladocera	–	5.9	16.7	–	40.0	18.5	90.9	93.3
Ostracoda	7.1	5.9	25.0	60.0	90.0	29.6	9.1	26.7
Cirripedia larvae	14.3	29.4	33.3	–	90.0	55.6	45.5	20.0
Malacostraca								
Amphipoda								
Gammaridea	92.9	94.1	70.8	60.0	40.0	59.3	18.2	26.7
Caprellidea	78.6	76.5	33.3	20.0	–	22.2	18.2	6.7
Cumacea	57.1	52.9	37.5	40.0	10.0	11.1	9.1	6.7
Tanaidacea	50.0	35.3	29.2	20.0	10.0	7.4	18.2	–
Isopoda	7.1	5.9	8.3	–	–	3.7	–	–
Mysidacea								
Mysida	7.1	–	8.3	60.0	–	3.7	–	–
Decapoda	7.1	17.6	33.3	60.0	10.0	37.0	54.5	46.7
Bivalvia	–	5.9	4.2	–	–	–	–	–
Gastropoda	–	5.9	8.3	20.0	–	–	–	–
Cephalopoda larvae	–	5.9	–	–	10.0	3.7	–	–
Ophiuroidea	7.1	–	–	–	–	25.9	–	40.0
Polychaeta	35.7	29.4	25.0	20.0	–	–	–	–
Fish eggs	14.3	23.5	8.3	20.0	50.0	37.0	45.5	33.3
Fish larvae	–	–	4.2	20.0	–	–	–	–

The number of fish examined in each class is as in Table 3.

Gammaridea intake were followed by those of Caprellidea intake; fish in the 50 mm and 60 mm classes showed considerably higher rates of Caprellidea intake. The rate of Caprellidea intake decreased to 33.3% when the fish were 70 mm. According to the point method, fish eggs had the third largest value, demonstrating that they were not a general main food item for 60 mm and 70 mm fish. The rate of planktonic Copepoda intake was high in the 50–90 mm size stages. At these stages, Cumacea and Tanaidacea also showed high rates (Table 5). These findings suggest that the solitary fish foraged mainly on small benthic animals, such as, Gammaridea and Caprellidea. However, with growth, the solitary fish consumed various food items, such as, fish eggs, which were consumed in large amounts by a small number of fish, and Copepoda, which were consumed in small amounts by a large number of fish. Small amounts of fine sand were found in the stomach contents of 26 of 61 fish.

The rate of Copepoda and Appendicularia intake among aggregative fish in size classes 40 mm to 70 mm FL was high (Table 5). The intake rate of Cladocera, as well as that of planktonic ani-

mals, was 40% in the 40 mm size class. This rate decreased in the 50 mm size class, but increased at the 60 mm and 70 mm size classes. According to both the numerical and points methods, the rate of Cladocera intake of 70 mm size class fish was the highest, showing that this food item was very important for fish at this stage of development. No fine sand was found in the stomach content of aggregative fish.

### Index of relative importance

The IRI values of the five main food items: Copepoda, Appendicularia, Cladocera, Gammaridea and Caprellidea are given in Table 6. In solitary fish, Copepoda, Gammaridea and Caprellidea comprised the main food items. Copepoda showed the largest value in the 60 mm FL size class, but this value decreased in larger fish. Gammaridea constantly showed larger values, but in the 80 mm size class the value was smallest. Caprellidea showed the largest value in the 50 mm size class, however, these values tended to be smaller in larger size

**Table 6** Changes in values of index of relative importance (IRI) of food composition with growth

Fork length class (mm)	Solitary				Aggregative			
	50	60	70	80	40	50	60	70
Food items								
Copepoda	4060	8421	2632	1528	16 930	15 440	5420	2 071
Appendicularia	390	107	515	108	2 529	3 349	5553	4 581
Cladocera	0	0	61	0	4	1	7435	11 559
Gammaridea	5657	3462	3717	2334	4	112	5	8
Caprellidea	4032	2149	879	1364	0	4	1	0

Figures below a decimal point omitted.

classes. Appendicularia and Cladocera, especially Cladocera, were disregarded due to small IRI values.

In aggregative fish, Copepoda was the main food item in the 40 mm and 50 mm FL size classes, but in larger fish its importance decreased. In contrast, Cladocera composed the main food item in the 60 mm and 70 mm size classes, however, consumption in the 40 mm and 50 mm size classes was negligible. Appendicularia was consistently consumed, with IRI values tending to increase with growth. The other two food items, Gammaridea and Caprellidea, were disregarded as prey of this behavioral type of fish.

## DISCUSSION

The feeding territories of juvenile *E. japonica* and *P. major* have been observed in natural waters.<sup>10–12</sup> The present study clearly shows that from May to June, the solitary, territorial fish have greater fork length and condition factor values than aggregative, nonterritorial fish (Tables 1,2). Some think that larger, well-nourished fish hold a territory and the present results do not necessarily indicate an advantage of holding a territory for better growth and condition. We assume that these larger values found in the solitary fish can be attributed to the effect of prior residence intermediated by territorial behavior, which regulates the carrying capacity of red sea bream.<sup>15</sup> In red sea bream, it has been experimentally shown that territorial juveniles grow better and are in better condition than nonterritorial juveniles.<sup>19</sup> The existence of a carrying capacity for crimson sea bream was also supposed.<sup>6</sup> Hence, the early settlement of juvenile solitary fish into a sandy substrate to hold territory seems to result in better growth. Therefore, the aggregative fish function as reserve members to hold the territory in case of the appearance of vacant territories. The RAPD-PCR method showed that the average band sharing index (BSI) of red sea bream was very high (0.817),<sup>20</sup> suggesting that

intraspecific genetic differentiation is very low and the two types cannot be discriminated genetically at all.

According to the occurrence method stomach content analyses carried out on juvenile *E. japonica* from Shijiki-Bay, the rate of Copepoda intake of fish smaller than 50 mm FL was higher than 90%. However, this rate decreased dramatically to about 10% in 80–90 mm FL fish.<sup>21</sup> A similar decrease in the rate of Copepoda intake, as measured by the occurrence method with growth, was not observed in either solitary or aggregative fish in the present study. However, values of IRI support that the relative importance of Copepoda is low in larger juveniles of both types (Table 6).

The results of the Shijiki-Bay observations, as given by the numerical method, showed that fish smaller than 60 mm FL foraged mainly on Copepoda. Fish larger than 60 mm FL consumed a smaller number of Copepoda and instead fed mainly on Gammaridea.<sup>21</sup> In the present study, aggregative fish showed a similar change in the rate of Copepoda intake (Tables 3,4), however, the most prevalent prey for larger individuals was not Gammaridea (benthos), but both Cladocera and Appendicularia (zooplanktonic organisms; Tables 3,4). The IRI values also support these facts (Table 6). In contrast, the rate of Copepoda intake of solitary fish decreased in individuals larger than 70 mm FL and Gammaridea intake became prominent; these results agree with those observed in Shijiki-Bay.<sup>21</sup> This suggests that fish used for stomach content analyses of juvenile crimson sea bream from Shijiki-Bay might have included both aggregative individuals mainly feeding on zooplanktonic organisms and solitary fish that mainly fed on benthic organisms.

The two behavioral types of fish should be identified in studies of food intake preferences among juvenile crimson sea bream. This is especially important when considering interspecific relationships between red sea bream and crimson sea bream sharing a nursery ground. Only solitary crimson sea bream have a competitive relationship

with juvenile red sea bream because the most prevalent prey of both is Gammaridea.<sup>22–24</sup>

The changes in food intake with growth in crimson sea bream may be related to the interspecific competition between the two species. According to Kudoh and Yamaoka<sup>10</sup> and Kudoh,<sup>19</sup> the two species do not form interspecific territories; their territories overlap. However, aggressive behavior was observed between the two species.<sup>10</sup> The feeding behavior of solitary individuals of the two species differed, with crimson sea bream tending to forage more frequently in the water column more than 50 cm above the sandy substrate, compared to red sea bream.<sup>11</sup> The frequency of each solitary individual in its own territory during a given period was greater in red sea bream than in crimson sea bream.<sup>19</sup> This suggests that red sea bream have a stronger affinity to substrate-associated territory than crimson sea bream. It is likely that only larger individuals of crimson sea bream can form a territory in interactions with red sea bream. Red sea bream became territorial at 30 mm, whereas territoriality appeared in crimson sea bream >50 mm.<sup>19</sup>

Aggregative fish preyed mainly on planktonic organisms, because there seems to exist a carrying capacity intermediated by the territorial behavior of juvenile crimson sea bream,<sup>10</sup> as has also been observed in red sea bream.<sup>15</sup> Aggregative fish cannot form territories, which makes it impossible for them to prey on benthic organisms.

No fine sand was found in the stomach contents of aggregative fish. In contrast, a small amount of fine sand was found in about half of the solitary fish (26 of 61). This finding, when considered together with the observation that aggregative fish were more dependent on planktonic organisms than were solitary fish (Table 6), suggests that the former type usually takes food from a water column. This is also supported by the observed behavior of juvenile crimson sea bream, namely, that the aggregative fish swam in the water column 1–4 m away from the bottom and appeared to select planktonic organisms.<sup>10</sup>

Fine sand found in the stomach of solitary fish was probably consumed during foraging on the sandy substrate (i.e. while sand pecking and digging).<sup>11</sup> However, solitary fish sometimes also consumed planktonic organisms in the water column greater than 50 cm from the substrate, which explains why not all solitary fish had fine sand in their stomach contents.<sup>11</sup>

Ecological researchers studying the feeding behavior of fish should be aware that fine sand may be present in the stomach, because such data can be very informative with regards to making inferences about feeding behaviors. We consider feeding behavior more important than has previously

been assumed, especially in the context of attempting to understand the coexistence mechanism suggested by Yamaoka.<sup>25</sup>

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