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Effects of highly unsaturated fatty acids on escape ability from moon jellyfish *Aurelia aurita* in red sea bream *Pagrus major* larvae

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ABSTRACT: The development of escape behavior from moon jellyfish *Aurelia aurita* was studied in the red sea bream *Pagrus major* larvae raised with two distinct dietary regimes: one fed rotifers and *Artemia* nauplii enriched with highly unsaturated fatty acids (the HUFA-enriched group); and the other fed those without enrichment (the HUFA-deficient group). The length of time that it took for a larva to be captured by three medusae of *A. aurita* was measured. The observation was continued for 5 min. The capture time was compared between the two dietary groups for the same age, and among different ages within the same dietary group. The capture time in the HUFA-enriched group was significantly longer on day 18 and day 20 compared to the younger stages, whereas there was no such discernible developmental changes in the HUFA-deficient group. The average capture time on day 18 in the HUFA-enriched and HUFA-deficient groups was 277 and 161 s, respectively, with almost the same body length (7.1 mm and 7.2 mm, respectively). Fatty acid analysis revealed that rotifers and *Artemia* in the HUFA-enriched group contained 2.2 and 0.6% of docosahexaenoic acid (DHA) in dry weight, whereas those in the HUFA-deficient group did not contain any detectable amount of DHA. Present work revealed that *A. aurita* can be a potential predator of *P. major* up to lengths of 7.1 mm (day 18) when the nutritional condition of the fish was good, and that the threat can be serious up to larger sizes when the fish had experienced inferior dietary conditions.

KEY WORDS: ***Aurelia aurita*, behavioral ontogeny, docosahexaenoic acid, escape ability, highly unsaturated fatty acids, *Pagrus major*, predation.**

INTRODUCTION

Red sea bream *Pagrus major* is one of the most important fisheries resources along the Japanese coastal waters. Spawned around offshore reefs,[1] they spend 30–40 days in the planktonic larval period, then are transported to coastal shallow sandy areas (5–10 m water depth) to start demersal life. The amount of recruitment fluctuates more than one order of magnitude.[2–4] The typical diet in wild larvae and early juveniles consists of copepods such as *Acartia omorii* and *A. steueri*.[5]

In general, the amount and species composition of prey animals for fish fluctuate spatially and temporally, as does the nutritional quality of certain prey species. For example, the highly unsaturated fatty acid (HUFA), especially docosahexaenoic acid (DHA), content of copepods fluctuates dramatically in a relatively short period.[6–8] Considering that marine fish larvae require dietary HUFA supplement,[9] fluctuation of the nutritional quality could have a substantial impact on the growth, survival, and year-class strength of particular fish species. This would be especially so when the habitat of the larval stage is limited and dietary animal quantity and quality suffer measurable changes, such as in the case of the red sea bream.

The moon jellyfish *Aurelia aurita* is distributed worldwide from equatorial to polar waters.[10] A recent massive bloom of this species had detrimental effects on the coastal fisheries in Japan.[11] The jellyfish is also known to be a predator of fish larvae. Möller reported substantial incidence of herring *Clupea harengus* larvae in the *A. aurita*

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stomach contents[12] and suggested a negative correlation between the amount of *A. aurita* and the herring population.[13] Laboratory studies also suggested a potential impact of *A. aurita* as predators; they feed on the larvae of herring,[14–17] Atlantic cod *Gadus morhua*, flounder *Platichthys flesus*, plaice *Pleuronectes platessa*,[16,17] turbot *Scophthalmus maximus*[17] and capelin *Mallotus villosus*.[18–20] Pepin *et al.*, however, suggested that the jellyfish is a less efficient predator than a piscine predator such as the stickleback on larval capelin.[21] Here we could expect that fish larvae are vulnerable to predation by jellyfish up to a certain stage and/or when the condition of the fish is not good enough to avoid predation by jellyfish.

In the present study we investigated the developmental changes of escape ability in the red sea bream larvae against the moon jellyfish. Fish were reared with one of two distinct dietary conditions, either HUFA-enriched or HUFA-deficient, to determine the effect of dietary condition on development of antipredator performance.

MATERIALS AND METHODS

Fish husbandry

Naturally spawned and fertilized red sea bream eggs were provided by Kyoto Prefectural Sea-Farming Center on 3 July 2001. Approximately 60 000 eggs were transferred to Fisheries Research Station of Kyoto University, and equally divided into four black circular polycarbonate 500 L holding tanks. The eggs were kept at ambient temperature (24.5°C) and hatching occurred on the same day.

From day 2, fish in two of four tanks were provided with rotifers *Brachionus plicatilis* cultured with freshwater chlorella (Nama-Chlorella V12; Kyowa Hakko Kogyo, Tokyo, Japan) and enriched with commercial HUFA oil (Docosa EM, Akita Jujo Kasei, Akita, Japan) for 9 h with a density of 5 ind./mL (HUFA-enriched group). Fish in the other two tanks were fed rotifers at the same density but without any enrichment (HUFA-deficient group). *Nannochloropsis* was added to each holding tank at a density of approximately 100 000 cell/mL up to day 3. From day 15, *Artemia* spp. nauplii were fed with a density of 0.5 ind./mL in addition to rotifers in all tanks, again with or without HUFA enrichment. The HUFA enrichment period of *Artemia* was 9 h. Rearing was conducted up to day 20, during which the water temperature ranged from 24 to 27°C and the light intensity of the water surface in the daytime was approximately 500 lx.

Jellyfish collection and husbandry

We collected *A. aurita* in Maizuru Bay by snorkeling at depths of 2–10 m at 50–300 m offshore from Fisheries Research Station of Kyoto University, Maizuru, Kyoto. After being captured in a transparent plastic bag, jellyfish were transported into the laboratory immediately. They were then kept in two 100 L holding tanks at natural water temperature for a few weeks until used for the experiment. Slow water-flow was provided but not aeration. The HUFA-enriched *Artemia* nauplii and red sea bream larvae were occasionally fed to satiation. Jellyfish were starved for at least 24 h before being used in the experiment.

Predator–prey experiment

Three actively pulsing jellyfish (60–88 mm in bell diameter) were selected, moved from holding tanks to a circular plastic experimental tank (30 cm in diameter, 10 L in volume) and were acclimatized for 10 min. The experimental tank was surrounded with a black plastic sheet to minimize the effect of the influence of observers. A relatively shallow depth of water (10 cm) prevented them from vertical movement, and gentle water flow along the tank wall facilitated the movement of jellyfish. Water was exchanged at 500 mL/min and the water temperature ranged from 24 to 27°C during the experiment.

Ten red sea bream larvae were taken out randomly from each dietary group (five from each tank) and put into the experimental tank one by one using a pipette, leaving a distance from each jellyfish as far as possible. Each trial was conducted alternately between two dietary groups. During the behavioral observation we measured how long it took for a larva to be captured by a jellyfish, defined as the capture time. When a fish touched a jellyfish but escaped from it and resumed a normal swimming behavior we did not consider it as a capture. In contrast, when a fish touched a jellyfish, escaped, but ceased to swim and became immobile, we regarded it as a capture. When a fish was captured within 5 s after the release, we considered that either the handling process influenced it or the releasing procedure was inappropriate, and discarded the data. We continued each observation up to 5 min when a fish continued to escape from jellyfish. In the case that a larva hid behind the inflow vinyl tube, which was a rare case, the fish was moved slowly from there to resume the swimming in the current. We replaced jellyfish and water when we finished the first 10 trials (five fish from one of two tanks in each dietary group), then con-

ducted another 10 trials using fish from different rearing tanks. The experiment was conducted every other day from day 2 to day 20, and from 13:00 hours to 15:00 hours on each day. To estimate the satiation level of the predator, a jellyfish (approx. 70 mm in bell diameter) was fed red sea bream (on day 20) that were anesthetized by cooling.

Twenty red sea bream larvae were sampled from each dietary group on each experiment day and their standard lengths (SL) were measured after anesthesia. They were fixed with 10% neutral formalin and were served to count dorsal and pectoral fin rays and to observe the osteological development of the vertebra and caudal skeleton after the double staining.[22]

The fatty acid compositions of rotifers and *Artemia* nauplii were analyzed by routine procedure.[23] Lipids were extracted according to Folch *et al.*[24] and were identified with gas chromatography (GC-15A; Shimadzu, Kyoto, Japan). Tricosanoic acid ($C_{23:0}$; Sigma Chemical, St Louis, MO, USA) was used for the internal standard.

Data from two tanks in each dietary group were combined for further analysis. The SL of fish among groups were compared by Student's *t*-test. Mann–Whitney *U*-test was applied to compare the capture times among different dietary groups, and Kruskal–Wallis test followed by Nemenyi test was applied to compare the capture time at different days after hatching within the same dietary group.[25]

RESULTS

The mean SL among groups were not significantly different up to day 18 ($P > 0.05$, Student's *t*-test). On day 20, the mean SL in the HUFA-enriched group was slightly smaller than that in the HUFA-deficient group ($P = 0.042$, Student's *t*-test; Fig. 1). The size range of fish on that day was 7.8–9.5 mm and 7.8–9.8 mm in the HUFA-enriched and HUFA-deficient groups, respectively.

The observations of osteological development of caudal bones showed no difference in the timing of the appearance of the 5th hypural bone and of agglutination of parhypural, the first hypural and the second hypural bone between the two dietary groups. Ossification of vertebral column in the HUFA-enriched group was observed earlier than that in the HUFA-deficient group when compared at the same SL (Fig. 2). Early juvenile stage, defined as the completion of dorsal and pectoral fin ray numbers and notochord flexion, was attained by 90% of individuals in the HUFA-enriched group and 100% of individuals in the HUFA-deficient group, on day 20.

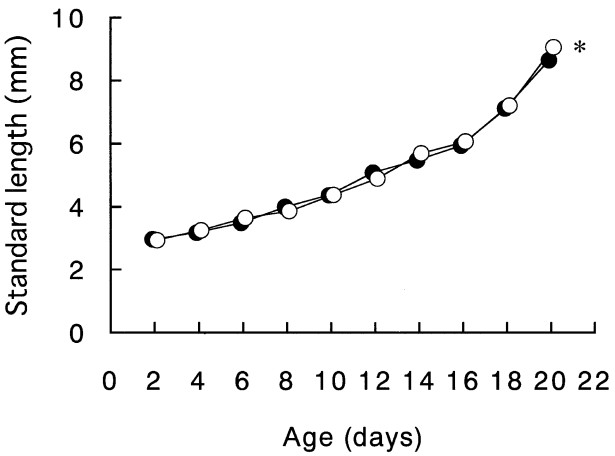

Fig. 1 Standard length of red sea bream in the highly unsaturated fatty acids (HUFA)-deficient group (○) and in the HUFA-enriched group (●). Values are means ± SE ($n = 20$). *Significant difference between the experimental group by Student's *t*-test ($P < 0.05$).

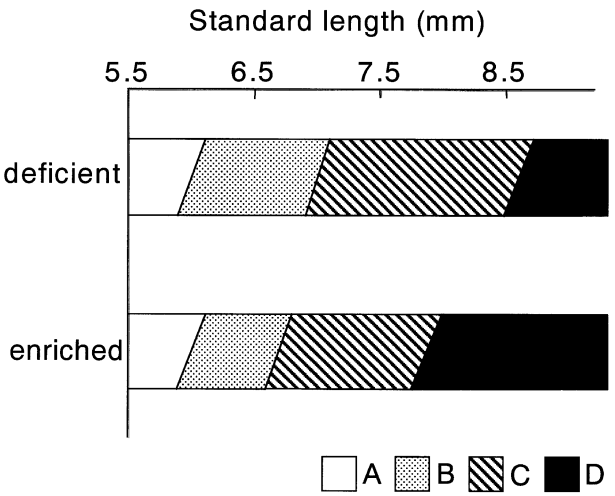

Fig. 2 Comparison of ossification process of vertebral column in the highly unsaturated fatty acids (HUFA)-deficient group (deficient) and the HUFA-enriched group (enriched). Ossification stages were classified as follows. A, ossification is not started yet while cartilage of vertebra and caudal skeleton is completed; B, neural arches start to ossify; C, centrums start to form; D, the 23rd centrum is completed and ossification is complete for the most part. Upper and lower edge of each column represent maximum and minimum size of fish in each stage.

On day 2, larvae in both groups hardly swam in the experimental tank so that jellyfish easily captured all the larvae. The escape abilities of larvae in both groups were not significantly different up to day 16. Five to nine individuals were captured in both groups. Larvae often hovered and kept the

same position unless a jellyfish approached. Jellyfish occasionally followed the movement of red sea bream.

In the HUFA-deficient group, mean capture time of red sea bream larvae by *A. aurita* was not significantly different when compared among different days (Kruskal–Wallis test; $P > 0.05$). In the HUFA-enriched group, in contrast, it was significantly different among ages; mean capture time on day 18 and on day 20 was significantly longer than those on previous days ($P < 0.01$, Kruskal–Wallis test followed by Nemenyi test). Mean capture time in the HUFA-deficient group was significantly shorter than that in the HUFA-enriched group on day 18 ($P < 0.01$; Mann–Whitney test) and on day 20 ($P = 0.018$; Mann–Whitney test; Fig. 3). Eight and five fish were captured on day 18 and 20 in the HUFA-deficient group, respectively, whereas only two on day 18 and one fish on day 20 were captured in the HUFA-enriched group.

Most larvae did not show any sign that they were detecting the approach of jellyfish, and some even approached a jellyfish by themselves. As fish became older, some individuals escaped from a jellyfish after touching its tentacles, oral robes or the surface of the exumbrella. In such cases a larva usually recovered and resumed normal swimming in a short period, whereas in some cases fish ceased to swim, sank to the bottom and soon died, probably because of the nerve venom of jellyfish. In the satiation trial one jellyfish ate 110 red sea bream larvae on day 20.

Fatty acid analysis revealed that HUFA-deficient rotifers or *Artemia* did not contain any detectable amount of DHA, whereas HUFA-enriched rotifers and *Artemia* contained 2.2% and 0.6% of DHA in dry weight, respectively (Table 1). The amount of eicosapentaenoic acid (EPA) was also very different, being high in the HUFA-enriched diet and low in the HUFA-deficient diet. Compositions of fatty acids in the diets are described in Table 2.

DISCUSSION

In the present study we demonstrated that (i) red sea bream larvae were easily captured by *A. aurita* regardless of dietary condition up to day 16; and that (ii) from day 18 or later, larvae fed HUFA-enriched diet were able to escape from *A. aurita*, whereas those fed HUFA-deficient diet continued to be captured. Our observation time in each trial was limited in 5 min so that the difference between the two dietary groups might have been larger than we observed. The amounts of DHA in HUFA-enriched rotifers and *Artemia* were comparable to those in wild copepods.[8]

Fukuhara and Kishida reported that the cruise swimming speed of red sea bream increases from

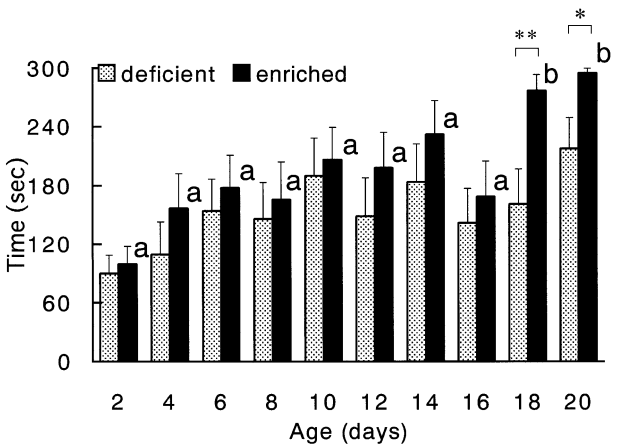

Fig. 3 Capture by *Aurelia aurita* on the red sea bream in each experimental group (means ± SE, $n = 10$). (▨), escaping time in the HUFA-deficient group; (■), escaping time in the HUFA-enriched group. Significant differences among experimental groups: Mann–Whitney test, $^{*}P < 0.05$; $^{**}P < 0.01$; different letters indicate significant differences within each dietary group (Kruskal–Wallis followed by Nemenyi test, $P < 0.05$).

Table 1 Fatty acid content (g/100 g dry weight) in the diets fed to red sea bream in the HUFA-deficient group and the HUFA-enriched group

	Rotifers		*Artemia* nauplii	
	Deficient	Enriched	Deficient	Enriched
Water (%)	85.5	86.8	86.7	89.9
Crude fat (%)	1.5	2.6	1.5	1.5
Crude fat in dry base (%)	10.3	19.5	11.4	15.2
Fatty acid content (g/100 g dry base)				
20:5n-3 (EPA)	Tr	2.8	0.1	1.2
22:6n-3 (DHA)	ND	2.2	ND	0.6
Σn-3HUFA	0.2	5.8	0.3	2.1

All crude fat is regarded as fatty acid. HUFA, highly unsaturated fatty acids; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; Tr, trace; ND, not detected (under detection limit); Σn-3HUFA, 20:4 + 20:5 + 22:6.

Table 2 Composition of fatty acids (% area) in the diets fed to red sea bream in the HUFA-deficient group and the HUFA-enriched group

	Rotifers		*Artemia* nauplii	
Fatty acid	Deficient	Enriched	Deficient	Enriched
14:0	2.9	2.4	1.2	1.4
16:0	11.5	10.5	11.7	9.2
16:1	2.5	4.8	5.9	6.4
18:0	1.7	1.8	4.4	2.3
18:1	1.7	1.4	15.3	9.1
18:2n-6	30.6	19.3	6.3	5.1
18:3n-6	1.0	0.8	ND	ND
18:3n-3	0.3	0.6	4.9	6.6
18:4n-3	0.4	0.3	0.2	0.3
20:3n-6	0.5	0.4	0.1	ND
20:4n-6	0.3	0.8	0.3	0.3
20:3n-3	0.8	0.5	0.5	0.3
20:4n-3	1.0	0.9	1.0	0.8
20:5n-3 (EPA)	0.2	14.1	0.9	7.9
22:4n-6	ND	1.3	ND	0.3
22:5n-6	ND	ND	ND	ND
22:5n-3	0.3	2.8	ND	0.6
22:6n-3 (DHA)	ND	11.2	ND	3.9
ΣMonoene	4.2	6.2	21.3	15.5
ΣSaturated	16.1	14.6	17.2	12.9
Σn-3	2.9	30.5	7.5	20.4
Σn-6	32.4	22.6	6.7	5.7
Σn-3HUFA	1.7	29.9	2.2	13.5

HUFA, highly unsaturated fatty acids; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; ND, not detected (under detection limit); Σn-3HUFA, 20:4 + 20:5 + 22:6.

approximately 150 mm/min at 3 mm SL to 300 mm/min at 6 mm SL,[26] corresponding to day 2 and day 16 in our experiment, respectively. We had expected that the increase of swimming speed should increase the rate of encountering predators and thus could result in high mortality at certain stages of larvae until they develop the proper escape capability. Although we observed a decreased capture time at day 16, this was not significantly different. Perhaps fish gradually developed their escape capability and this would have masked the increased risk induced by the increased encountering rate. Because predation by jellyfish would be related to both the encountering rate and the escape capability, a larger experimental tank may be required to be conclusive about this point.

The mean SL of the two groups were almost the same, although there was a slight difference between the dietary groups on day 20. This difference may be partly due to the high mortality of smaller individuals in the HUFA-deficient group. A high mortality of marine fish fed HUFA-deficient diets has been reported in several species such as red sea bream,[23,27] yellowtail *Seriola quinqueradiata*[28] and striped jack *Pseudocaranx dentex*.[29]

Aurelia aurita prey on planktonic animals contained in the water flowing into the subumbrella as it pulsates.[30] Therefore three factors should be required for avoiding this predation: sensory organs to detect the approach of jellyfish; swimming organs to escape; and a central nervous system (CNS) to coordinate behavior. Red sea bream larvae in the HUFA-deficient group were thought to lack at least one of these three factors.

Morphological observation revealed that the timing of ossification in the HUFA-deficient group was slightly behind that in the HUFA-enriched group. This may have induced the difference in swimming capability between those two groups. However, HUFA-deficient fish on day 20 had almost completed ossification but still failed to escape from the jellyfish, whereas HUFA-enriched fish on day 18 escaped well in spite of their incomplete ossification. Our previous work compared the burst and cruise swimming capability between two dietary groups of chub mackerel *Scomber japonicus* larvae, demonstrating that piscivorous larvae can swim faster than planktivorous larvae.[31] The difference was relatively small: 18.45 SL/s and 13.98 SL/s in the burst swimming in fish-fed and zooplankton-fed group, respectively. Bailey con-

ducted laboratory experiments on the predation of Atlantic cod, flounder, plaice, herring and turbot by *A. aurita*, and demonstrated that the predation rate by *A. aurita* was not closely correlated to the swimming speeds of larvae.[17] Furthermore, we observed that most larvae captured by jellyfish did not show escape behavior, suggesting that the difference in escape ability should have resulted from other factors than swimming ability.

Impairment of vision in HUFA-deficient animals has been reported from fish[32] to the monkey.[33] Bell *et al.* demonstrated that herring juveniles fed on a DHA-deficient diet were inferior in feeding ability under low light intensity (0.1–1.0 lx) due to the maldevelopment of the rod cells in the retina.[32] In the present experiment, however, light intensity was set at approximately 500 lx, which was well above the light intensity threshold of vision. Even in this condition, fish larvae from either group did not show much sign of visual reaction to the approach of jellyfish. This was probably because, as Bailey and Batty pointed out, the jellyfish was not easy to detect because of its transparency.[16]

Free neuromasts are the primary sensory organ to detect the movement of water flow in fish larvae, and the formation of buccal and lateral canals will facilitate the detection of direction.[34] We observed free neuromasts in fish as early as day 2 in both groups, whereas development of canals will be later than day 20.

Masuda *et al.* demonstrated that radioisotope-labeled DHA was incorporated into the CNS in yellowtail.[35] It is likely in the present experiment that HUFA deficiency resulted in the delay of CNS development. Because of this they might have failed to react to approaching predators and assess the safe distance, resulting in the higher capture rate by the jellyfish.

Our satiation trial revealed that one jellyfish could consume at least 110 of the red sea bream larvae on day 20. Möller reported that field-collected *A. aurita* (42 mm in bell diameter) had 68 individuals of herring larvae.[13] *Aurelia aurita* is a coastal species and dominates mainly in eutrophic and inner-bay areas.[36] While red sea bream larvae are distributed mainly in the coastal open sea, they are reported to assemble in a geometric counter-clockwise circulation and become high in density near the opening of a bay in the case of Shijiki Bay, south-west of Japan.[2] *Aurelia aurita*, although a coastal species, may spread out to the front to the open sea, where they are likely to encounter fish larvae such as red sea bream. Considering such typical distributions of *A. aurita* and red sea bream together with our present results, predation mortality of red sea bream by moon jellyfish may well occur. Furthermore, because HUFA contents of copepods fluctuate,[6–8] red sea bream larvae that have experienced a nutritionally inferior diet may suffer even more serious mortality.

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