ゴマアイゴ仔魚の栄養転換

誌名	日本水産學會誌
ISSN	00215392
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発行元	日本水産學會
巻/号	54巻7号
掲載ページ	p. 1083-1091
発行年月	1988年7月

Nippon Suisan Gakkaishi 54(7), 1083–1091 (1988)

Transition from Endogenous to Exogenous Nutrition Sources in Larval Rabbitfish *Siganus guttatus*[*1]

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(Received June 19, 1987)

The early larval development of *Siganus guttatus* was studied with emphasis on the transition from endogenous to exogenous feeding. Three rearing trials were conducted as follows: 1) rearing in a 5 ton concrete tank at 27.9–29.3°C (T-85 trial); 2) rearing in a 0.5 ton fiberglass tank at 22.2–26.5°C (T-86A trial); 3) rearing in the same manner as in T-86A but without food (T-86B trial). On the basis of the developmental events and energy flow in T-86A trial, the early life history of the species could be divided into the following seven phases: 1) rapid larval growth due to rapid yolk resorption (from hatching to about 15 h after hatching (time after hatching: TAH)); 2) slow growth and organogenesis based mainly on yolk energy (to about 50 h TAH); 3) slow growth based on energy of yolk, oil globule and exogenous food (to about 70 h TAH); 4) slow growth based on two sources of energy, oil globule and exogenous food (to about 90 h TAH); 5) the same mode of development and energy flow as in the preceding phase, but with a certain level of feeding amount (to about 120 h TAH); 6) accelerated larval growth and effective feeding and swimming based only on exogenous food (to about 150 h TAH); and 7) the same mode as in the preceding phase with accelerated increase of feeding amount (beyond 150 h TAH). Differences in developmental mode were observed in T-85 and T-86A trials, but it could not be ascertained in this particular study which of the environmental factors played the greatest influence. The results of T-86A and B showed that the larvae, in order to survive, have to get over two obstacles on feeding, that is, to start feeding and to change from endogenous to exogenous feeding suitably.

Rabbitfish *Siganus guttatus* (Bloch) is widely distributed in the tropical and subtropical Indo-Pacific, and its habitats are diversified from estuarine waters to coral reefs. The species has been considered as a potential fish for aquaculture.[1] The spawning and larval rearing have been reported by many workers.[2–4] Despite the accumulation of a great deal of knowledge on its seed production at the Aquaculture Department of the Southeast Asian Fisheries Development Center (SEAFDEC), as reported by Hara *et al.*,[3] the task to maintain high survival rates still remains to be solved. Recent study on the transition from endogenous to exogenous feeding in larval *Lates calcarifer* (Bloch) pointed out the stabilization of survival rates in early larval stages of the species in terms of energy flow.[5] Resorption of endogenous nutriment in larval *S. guttatus* has been studied by Bagarinao,[6] but without consideration of the energetics involved. It is the purpose of this study to examine the growth, morphological development, yolk and oil globule resorption, and initial feeding in early larval *S. guttatus*, with emphasis on the transition of energy sources.

Materials and Methods

Larvae used in this study came from the spawning and rearing facilities in the Aquaculture Department of SEAFDEC. The spontaneous spawning from which the present study material originates occurred on 1 April 1985 and on 21 January 1986. The facilities and methods for stocking the spawners and for inducing the spawning have been described by Hara *et al.*[3] The following three trials of larval rearing were undertaken for the study.

Trial-1 (T-85)

Spawning occurred on 1 April 1985 by a male of 295 mm total length (TL) and a female of

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318 mm TL. Eggs spawned were transferred into a 5 ton rectangular concrete tank as incubation/rearing tank. The initial number of larvae hatched in the tank was about 143000 (28.6 individuals/*l* of water). The larvae were reared until 8 April 1985 (day 6) at 33–34 ppt salinity and 27.9–29.3°C. Rotifers, *Brachionus plicatilis*, were offered as food from day 2 at a density of 5–10 individuals/m*l* of water. Green algae, *Chlorella* sp., was added as food for rotifers and as water conditioner. A total of 127 larvae (1.68–3.69 mm TL) was sampled. The time of hatching is standardized to 00: 00 2 April 1985.

Trial-2 (T-86A)

Spawning occurred on 21 January 1986 by a male of 259 mm TL and a female of 267 mm TL. Larvae hatched in the spawning tank were transferred into a 0.5 ton fiberglass tank for rearing and were reared until 29 January 1986 (day 7). The initial number of larvae was about 12000 (24.0 individuals/*l* of water). The rearing salinity was 34 ppt, while temperature range was 22.2–26.5°C. Rotifers were offered on day 2 at an initial density of 20 individuals/m*l*. Rotifer count was monitored daily without adding, and its density still ranged from 10–20 individuals/m*l* during the experiment. *Chlorella* was added as in T-85. A total number of larvae sampled was 235 (1.85–3.45 mm TL). The time of hatching is set at 03: 00 22 January 1986.

Trial-3 (T-86B)

Larvae from this trial came from and were reared in the same manners in T-86A, except that no food was given. The rearing was continued until all larvae died. Salinity was 34 ppt and water temperature ranged from 22.0–26.0°C. Sixty-seven larvae (2.65–3.04 mm TL) were sampled for this trial. The hatching time is set at 03: 00 22 January 1986.

At least 5 (usually 10) larvae were sampled from each rearing tank at different intervals. All observations and measurements were made in the fresh state. Measurements were made under a binocular microscope with an ocular micrometer, read to the nearest 0.01 mm. Measurements of the following items were made on all trials; total length, yolk length and height, and oil globule diameter. In addition, on T-86A, the larval mouth width and lorica width of the biggest rotifer in digestive tract were measured, and number of rotifers eaten was determined by dissection of larvae sampled daily at about 9: 00 in the morning. Daily sampling of rotifers was conducted from the rearing tank of T-86A from day 2, and the number and lorica width distribution of rotifers in the rearing tank were determined. The methods for computing the yolk and oil globule volumes followed Kohno *et al.*.[5] Survival rate was examined in all trials.

Results

Growth and Survival

The newly hatched larvae in T-85 were 1.74 mm TL on an average (N=10, SD=0.043 mm), while those in T-86A were 1.90 mm TL (N=10, SD=0.040 mm) (Fig. 1). The larvae grew rapidly after hatching and reached to 2.83 mm TL (N=5, SD=0.107 mm) at 21 h after hatching (time after hatching, TAH) in T-85 and to 2.91 mm TL (N=10, SD=0.066 mm) at 20 h TAH in T-86A. Based on the logarithmic plots in Fig. 1, the flection point was observed at about 22 h TAH (2.85 mm TL) in T-85 and at about 18 h TAH (2.90 mm TL) in T-86A, respectively (Table 1). Thereafter a negative growth was evident in T-85, while slow growth was shown in T-86A. Regression analysis of TL means plotted logarithmically indicated that the negative growth in T-85 went on up to 76 h TAH, and, during this period (54 h, 22–76 h TAH), the loss in TL was 0.35 mm. On the other hand, the larvae in T-86A grew slowly up to about 125 h TAH and reached to 2.97 mm TL at the time (the gain in TL was only 0.07 mm during the period of 107 h, 18–125 h TAH). Following the period of the negative or slow growth, the larvae grew acceleratedly; the average TL reached to 3.33 mm at 155 h TAH in T-85 (N=5, SD=0.300 mm; TL acquired was 0.83 mm during the period of 79 h, 76–155 h TAH), and in T-86A the TL reached to 3.36 mm on an average at 176 h TAH (N=7, SD=0.073 mm; the acquired TL was 0.39 mm during the period of 51 h, 125–176 h TAH).

The growth mode of larvae in T-86B (no food) showed the same pattern as in T-86A up to day 3 (Fig. 1). Thereafter the larvae tended to shrink, the average TL reached was 2.87 mm at 106 h TAH in T-86B (N=6, SD=0.075 mm), while it to 2.99 mm at 106.5 h TAH in T-86A (N=10, SD=0.071 mm). At 109.5 h TAH, the average TL decreased to 2.83 mm in T-86B (N=6, SD=0.049 mm), while it was 2.98 mm at 110 h TAH in T-86A (N=10, SD=0.083 mm).

The survival rates in three trials are shown in Fig. 2. Although the survival rate was examined only one time, at 144 h TAH, in T-85, it showed

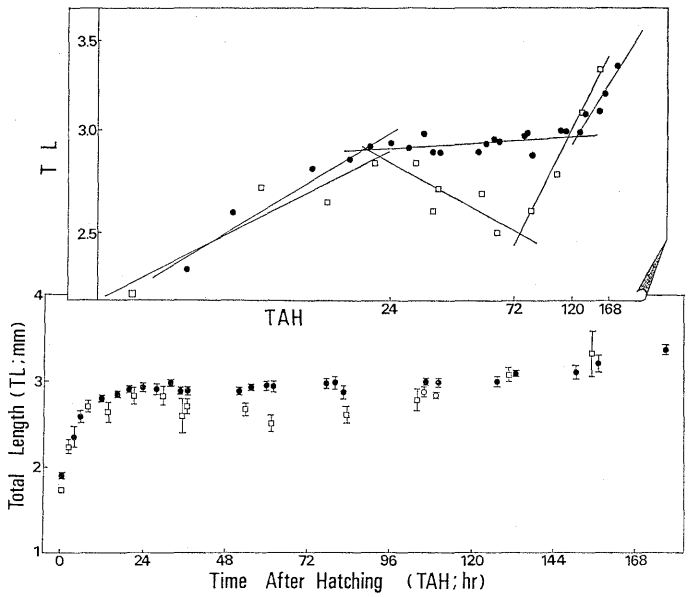

Fig. 1. Growth in larval *Siganus guttatus* of T-85 (open square), T-86A (solid circle) and T-86B (open circle) trials. Top: log-log plot of mean TL. Bottom: mean TL with 95% confidence limit (bar).

Table 1. Regression analysis for the growth in larval *Siganus guttatus* of two trials, T-85 and T-86A. The equation is $ln\,(TL)=a+b\cdot ln\,(\text{Time after hatching, TAH})$

TAH (h)	n	a	b	r*	Flection point	
					TAH (h)	TL (mm)
T-85 Trial						
– 22	4	0.737	0.101	0.930		
					21.78	2.85
22– 80	5	1.378	−0.107	−0.727		
					76.02	2.50
80–155	4	−0.794	0.394	0.995		
T-86A Trial						
– 20	5	0.703	0.125	0.976		
					18.04	2.90
20–127	16	1.027	0.013	0.517		
					124.69	2.97
127–176	5	−0.469	0.323	0.956		

* Correlation coefficient.

a remarkable low value, 0.62% (it should be noted that the average survival rate of other five rearing trials on the same spawning and facilities as in T-85 was quite low, 2.15%, N=5, SD=1.81%). The sudden decrease of survival was observed during the first 15 h after transferring the larvae to the rearing tank in both T-86A and T-86B trials. This decrease may be attributable largely to handling stress. In T-86A the survival rate bacame stable within 60–112 h TAH, but thereafter the survival rate decreased to 21.17% (N=3, SD=4.67%) at 112.0 h TAH and to 5.89% (N=3, SD=5.10%) at 160.0 h TAH. On the other hand, the survival rate decreased exponentially, and all larvae died up to 125 h TAH in T-86B.

Yolk and Oil Globule Resorption

The average yolk volume, which includes oil globule, of newly hatched larvae was 203.4×10^{-4} mm^3 (N=10, SD=48.96×10^{-4} mm^3) in T-85 and 239.2×10^{-4} mm^3 (N=10, SD=49.95×10^{-4} mm^3) in T-86A (Figs. 3 and 4). The average oil globule volume was, on the other hand, 42.9×10^{-4} mm^3 (N=10, SD=7.74×10^{-4} mm^3) in T-85 and $34.2\times$

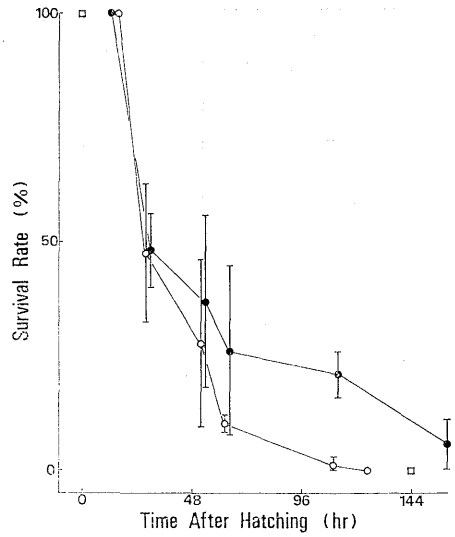

Fig. 2. Survival in larval *Siganus guttatus* of T-85 (open square), T-86A (solid circle) and T-86B (open circle) trials.

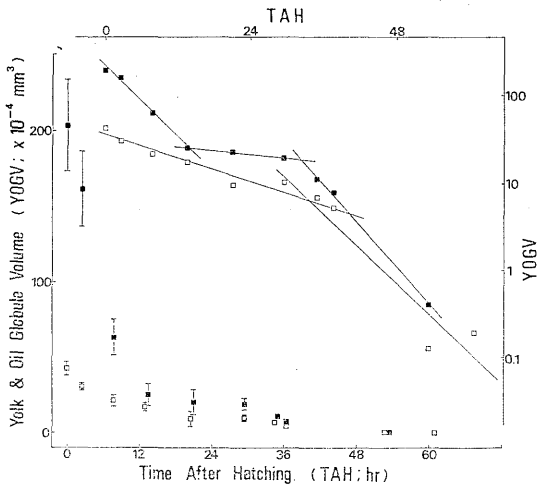

Fig. 3. Yolk (solid square) and oil globule (open square) resorption in larval *Siganus guttatus* of T-85 trial. Left-bottom: mean volume (square) with 95% confidence limit (bar). Right-top: semi-logarithmic plot of mean volume.

10^{-4} mm³ (N=10, SD=9.29×10^{-4} mm³) in T-86A. The mode of both yolk and oil globule resorption was almost the same in T-85 and T-86A, though the rate of resorption was different between them as mentioned below.

During the first several hours after hatching, the sudden decrease of yolk volume was perceived; in T-85 87.6% of the yolk was consumed by the first 13.5 h, and 94.2% by the first 24 h in T-86A. After this point, the resorption rate of yolk

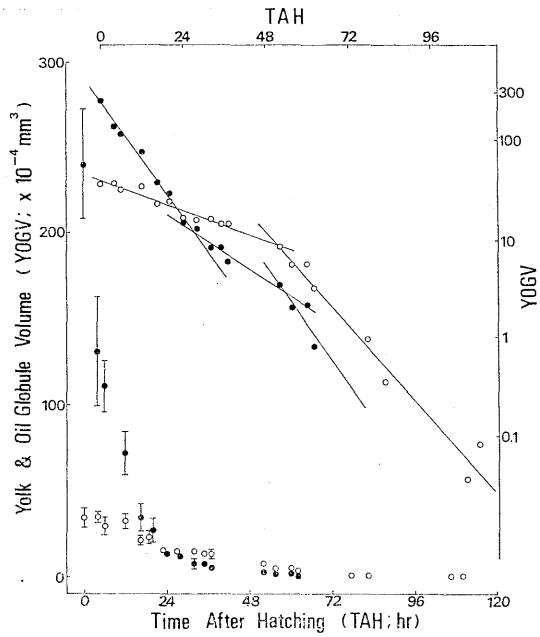

Fig. 4. Yolk (solid circle) and oil globule (open circle) resorption in larval *Siganus guttatus* of T-86A trial. Left-bottom: mean volume (circle) with 95% confidence limit (bar). Right-top: semi-logarithmic plot of mean volume.

became slow and this continued up to 32 h TAH in T-85 and up to 54 h TAH in T-86A. During this period of two flection points in semilogarithmic plots (Figs. 3 and 4; Tables 2 and 3), the loss in yolk volume was 6.6×10^{-4} mm³ in T-85 (18 h, 14–32 h TAH) and 8.4×10^{-4} mm³ in T-86A (27 h, 27–54 h TAH). Thereafter the rate of yolk resorption was fast again, and the yolk was completely exhausted during the period 54–61 h TAH in T-85 and 62–78 h TAH in T-86A.

With regard to oil globule resorption, on the other hand, one flection point was recognized in both T-85 and T-86A trials on the basis of semilogarithmic plots (Figs. 3 and 4). The flection point was situated at 33 h TAH in T-85 and 51 h TAH in T-86A (Tables 2 and 3). From hatching till this point, the slope of the regression line was gentle, though the loss was 84.8% in T-85 (0–33 h TAH) and 75.4% in T-86A (0–51 h TAH). The rate of oil globule resorption became rapid after the flection point in both T-85 and T-86A, and the oil globule disappeared during the period 61–83 h TAH in T-85 and 110–127 h TAH in T-86A.

The resorption of yolk in T-86B trial (no food) showed almost the same pattern as in T-86A (Table 4). However, the rate of oil globule resorption in T-86B was different from that in T-86A

Table 2. Regression analysis for the resorption of yolk and oil globule in larval *Siganus guttatus* of T-85 Trial. The equation is ln (Volume)$=a+b\cdot$Time after hatching (TAH)

TAH (h)	n	a	b	r*	Flection point	
					TAH (h)	Volume ($\times 10^{-4}$ mm^3)
Yolk						
–13.5	4	5.388	−0.159	−0.997		
					13.79	24.40
13.5–30	3	3.436	−0.018	−0.953		
					31.96	17.75
30–54	3	8.587	−0.179	−0.100		
Oil globule						
–29.5	6	3.568	−0.051	−0.952		
					33.14	6.49
29.5–61	5	6.872	−0.151	−0.961		

* Correlation coefficient.

Table 3. Regression analysis for the resorption of yolk and oil globule in larval *Siganus guttatus* of T-86A Trial. The equation is ln (Volume)$=a+b\cdot$Time after hatching (TAH)

TAH (h)	n	a	b	r*	Flection point	
					TAH (h)	Volume ($\times 10^{-4}$ mm^3)
Yolk						
– 29	7	5.439	−0.112	−0.993		
					26.98	11.21
29– 57	6	3.847	−0.053	−0.975		
					53.52	2.75
57– 67	4	7.058	−0.113	−0.846		
Oil globule						
– 57	12	3.619	−0.029	−0.975		
					51.35	8.41
57–115	9	6.803	−0.091	−0.980		

* Correlation coefficient.

Table 4. Remained volume of yolk and oil globule (mean±SD; $\times 10^{-4}$ mm^3) in larval *Siganus guttatus*, comparing between T-86A (food provided) and T-86B (without food) Trials. Numerals in parentheses represent the ratio of larvae possessing each nutriment to those consumed up it

TAH* (h)	T-86A	T-86B
Yolk		
55.5	1.53±0.892 (70%)	2.26±0.898 (90%)
59.5	1.91±1.743 (70%)	2.26±1.989 (60%)
62	0.93±0.244 (30%)	0.55±0.116 (20%)
78	— (0%)	— (0%)
Oil globule		
62	3.83±1.312 (100%)	3.78±1.786 (100%)
78	0.93±0.768 (100%)	1.14±0.738 (100%)
82.5	0.35±0.293 (70%)	1.17±0.898 (100%)
106.5	0.04±0.022 (30%)	0.20±0.088 (83%)
110	0.08 (N=1) (10%)	0.10±0.088 (83%)
127	— (0%)	all larvae died up to 120 h TAH

* Time after hatching.

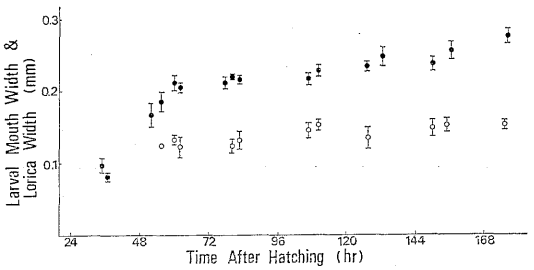

Fig. 5. Mean larval mouth width (solid circle) and mean lorica width of the biggest rotifer eaten (open circle) in larval *Siganus guttatus* of T-86A trial. Bar: 95% confidence limit.

(Table 4): by 82.5 h TAH 30% of larvae consumed up the oil globule in T-86A, while all larvae in T-86B still had the oil globule; and only one of ten larvae had the oil globule at 110 h TAH in T-86A, but 83% of larvae had it at the same time in T-86B. The larvae in T-86B consumed the remaining oil globule slower than those in T-86A.

Initial Feeding

Experiment on initial feeding was conducted for the larvae in T-86A. The larval mouth width, lorica width of the biggest rotifer eaten by larvae, number of rotifers in the digestive tract of larvae, and number and lorica width distribution of rotifers in the rearing tank were examined.

The opening of mouth was first evident in six out of ten larvae at 35 h TAH, and the average mouth width was 97.5 μm (N=6, SD=9.01 μm) (Fig. 5). With growth, the mouth width increased rapidly up to about 60 h TAH, at which time the average mouth width reached to 212.3 μm (N=10, SD=11.02 μm). Thereafter the increase of mouth width became slow up to about 130 h TAH, ranging 200–240 μm. There followed an accelerated increase in the subsequent stages, and the mouth width reached to 278.2 μm on an average at 176 h TAH (N=7, SD=13.34 μm).

The first perceived rotifer eaten was in the digestive tract of a 3.01 mm TL larva with 200.0 μm mouth width, sampled at 55.5 h TAH, and the lorica width of the rotifer was 125.0 μm (62.5% of the mouth width). At about the same time, 52.5 h TAH, the average number of rotifers in the rearing tank was 19.4 individuals/m*l* of water (N=5, SD=7.40 individuals), and the rotifers with less than 130 μm lorica width constituted about 70% of the total number of rotifers in the tank. Thus the available number of rotifers for the larvae was 13.6 individuals per m*l* of water. Throughout the experimental period, up to 176 h TAH, the lorica width of rotifers eaten ranged constantly between 110–160 μm (55–70% of the mouth width in the examined larvae), and the available rotifer number in the tank for larvae to feed was constant at 10–20 individuals per m*l* of water.

Fig. 6 shows the increase of number of rotifers in the digestive tract of larvae with growth. As mentioned above, the first feeding was evident at

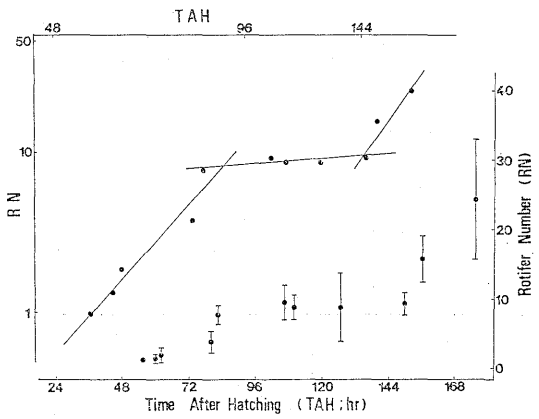

Fig. 6. Feeding amount (number of rotifers eaten) in larval *Siganus guttatus* of T-86A trial. Right-bottom: mean feeding amount (solid circle) with 95% confidence limit (bar). Left-top: log-log plot of mean feeding amount.

Table 5. Regression analysis for the food incidence in larval *Siganus guttatus* of T-86A Trial. The equation is *ln* (Rotifer number, RN)=$a+b\cdot ln$ (Time after hatching, TAH)

TAH (h)	n	a	b	r*	Flection point	
					TAH (h)	RN
– 76.5	5	−17.954	4.470	0.967		
					88.75	8.15
76.5–132	5	0.873	0.273	0.732		
					147.22	9.35
132 –172	3	−25.634	5.583	0.951		

* Correlation coefficient.

55.5 h TAH. All larvae started to feed by 82.5 h TAH, with 1–8 rotifers per digestive tract. The average number of rotifers eaten plotted logarithmically indicates that it increases till about 89 h TAH (Fig. 6 and Table 5). The number of rotifers remained at about 10 individuals per digestive tract up to about 150 h TAH (147.22 h TAH on the basis of the log-log plots). Thereafter an accelerated increase in feeding amount was observed, and the average number reached to 24.3 individuals per digestive tract at 176 h TAH (N=7, SD=11.74 individuals).

Development of Morphology

Larval development of *Siganus guttatus* has already been described by Hara *et al.*[4] by using the same material as in T-85 of the present study. In this study the development of principal feeding- and swimming-related characters was briefly compared between the larvae of T-85 and T-86A trials.

Eye lens and auditory vesicles were already seen in the newly hatched larvae in both T-85 and T-86A trials. By 6 h TAH six pairs of cupulae appeared on head and body in both trials. The pectoral fin buds appeared by 13 h TAH in T-85, though they appeared first at 16.5 h TAH in T-86A. Eyes commenced to be pigmented at 20 h TAH in T-86A. In T-85 eyes were completely pigmented by 24 h TAH, though the start of pigmentation was not observed. The completely pigmented eyes were evident by 32 h TAH in T-86A. Openings of mouth and anus were first recognized at 24 h TAH in T-85, while these were evident at 35 h TAH in T-86A. By 52 h TAH, digestive tract was coiled, and the mouth and pectoral fins were movable in T-86A.

Discussion

The development of early larval *Signus guttatus* in T-86A trial observed in this study is summarized as below and schematically epitomized in Fig. 7.

The rapid early growth of larvae depended on the rapid yolk resorption, both of which continued to about 15 h TAH. Organ differentiation was not seen during this period, and thus all the nutriment of the yolk resorbed was devoted to larval growth in length, except for the basic metabolism. The larval growth levelled off subsequently, up to

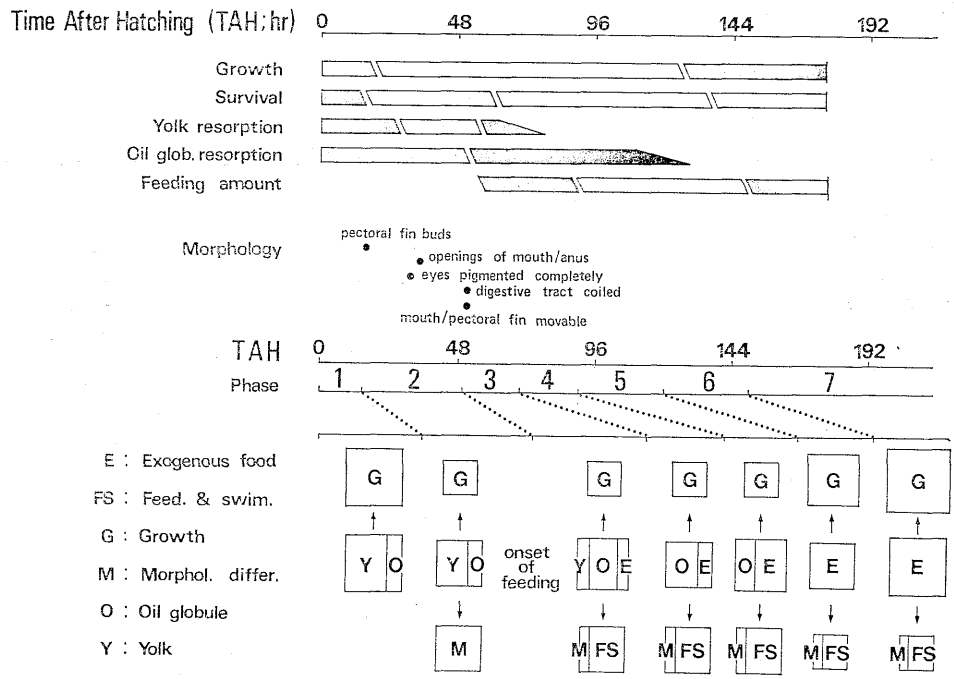

Fig. 7. Scheme of development (top) and schematical chart of energy flow (bottom) in larval *Siganus guttatus* of T-86A trial. The deeper shade in quadrangles indicates the higher rate of increase in growth and feeding amount and that of decrease in survival and yolk and oil globule resorption. Size of squares shows appropriate magnitude of revenue and expenditure of energy. For phase, see text.

about 125 h TAH, during which period, 15–125 h TAH, principal events of development took place successively. Oil globule, which was resorbed at a slow rate from the hatching, commenced to be consumed at a faster rate at about 50 h TAH, and this coincided with the first feeding and with a faster resorption of yolk. Prior to these events, the following morphological developments were seen: the pectoral fin buds appeared at 16.5 h TAH; eyes were completely pigmented at 32 h TAH, and mouth and anus opened at 35 h TAH; and at 52 h TAH digestive tract was coiled, and mouth and pectoral fins were movable. Survival rate became stable at about 60 h TAH, and yolk resorption was complete at period of 62–78 h TAH. Feeding amount reached to a certain level at about 90 h TAH, the level was maintained up to about 150 h TAH, and thereafter an accelerated increase in feeding amount was observed. Prior to the accelerated increase in feeding amount, the oil globule was completely exhausted at period of 110–126 h TAH. Larval growth was accelerated after about 125 h TAH, and high mortality was again seen after about 135 h TAH.

The scheme of energy flow in larval *Siganus guttatus*, based on the above-mentioned development scheme, is also shown in Fig. 7. The basic metabolism is not considered in the figure.

On the basis of the energy flow, the early life history of *Siganus guttatus* may be divided into seven phases as follows: 1) rapid larval growth due to rapid yolk resorption (from hatching to about 15 h TAH); 2) slow growth and organogenesis based mainly on yolk energy (to about 50 h TAH); 3) slow growth based on energy of yolk, oil globule and exogenous food (to about 70 h TAH); 4) slow growth based on two sources of energy, oil globule and exogenous food (to about 90 h TAH); 5) the same mode of development and energy flow as in the preceding phase, but with a certain level of feeding amount (to about 120 h TAH); 6) accelerated larval growth and effective feeding and swimming based only on exogenous food (to about 150 h TAH); and 7) the same mode as in the preceding phase with accelerated increase of feeding amount (beyond 150 h TAH).

However, a great difference was observed in the developmental mode of T-85 and T-86A trials. The negative growth was evident during the period 22–76 h TAH in T-85. Although the larval growth was very slow during the period 18–125 h TAH in T-86A, no negative growth was observed. The yolk and oil globule disappeared in earlier larval stages in T-85 (54–61 and 61–83 h TAH, respectively) than in T-86A (62–78 and 110–127 h

Table 6. Comparison of developmental events in larval *Siganus guttatus* between T-85 and T-86A Trials

	T-85	T-86A
Rearing conditions		
Spawner (mm in TL)	318	267
Rearing tank (ton)	5.0	0.5
Temperature of rearing water (°C)	27.9–29.3	22.2–26.5
Growth & Survival		
Early rapid growth	up to 22 h TAH	up to 18 h TAH
Negative growth	seen between 22–76 h TAH	not seen, but slow growth seen between 18–125 h TAH
Survival rate	0.62% at 144 h TAH	5.89% at 160 h TAH
Yolk & oil globule resorption		
Yolk	disappeared at 54–61 h TAH	disappeared at 62–78 h TAH
Oil globule	disappeared at 61–83 h TAH	disappeared at 110–127 h TAH
Appearance of characters		
Pectoral fin buds	13 h TAH	16.5 h TAH
Completely pigmented eyes	24 h TAH	32 h TAH
Openings of mouth and anus	24 h TAH	35 h TAH
Feeding incident		
Initial feeding	at 24 h TAH	at 55.5 h TAH
Time from mouth open to oil globule exhaustion	59 h	92 h
Time from initial feeding to oil globule exhaustion	59 h	71.5 h

TAH, respectively). The development of feeding- and swimming-related characters in T-85 preceded that in T-86A: pectoral fin buds appeared at 13 h TAH in T-85 and 16.5 h TAH in T-86A; eyes were completely pigmented at 24 and 32 h TAH, respectively; and the mouth and anus opened at 24 and 35 h TAH, respectively. Larvae started to feed earlier in T-85 (24 h TAH) than in T-86A (55.5 h TAH). However, based on the times from mouth opening and initial feeding to oil globule exhaustion, T-86A had greater time leeway to improve the energy sources from endogenous to exogenous; the time from opening of mouth to oil globule exhaustion was 92 h in T-86A and 59 h in T-85, and that from initial feeding to oil globule exhaustion was 71.5 h in T-86A and 59 h in T-85. The survival rate was very different between the two trials; 0.62% at 144 h TAH in T-85 and 5.89% at 160 h TAH in T-86A. There are some factors that would have played on the diversities of developmental mode in both trials, e.g. spawners, rearing tanks, rearing conditions, and so on. Although it could not be determined which factor had the greatest influence on these diversities, it should be bore in mind that intraspecific developmental mode exists as easily affected by environmental changes.

The importance of exogenous food was clearly shown by the survival rates obtained in T-86A and T-86B (Fig. 2). The survival rate decreased exponentially up to 50–60 h TAH in the two trials. Thereafter the survival rate continued to decrease exponentially in T-86B, while it became stable in T-86A. This point, about 60 h TAH, coincided with the onset of feeding in T-86A, 55.5 h TAH. Thus the larvae with stable survival rate in T-86A may benefit from the exogenous food. After the stable state, however, the survival rate decreased again during the period 110–160 h TAH in T-86A. Considering that all larvae in T-85B died up to 125 h TAH, we can infer that the failure to change from endogenous to exogenous feeding caused the decrease of survival rate. These results suggest that larvae have to get over two obstacles on feeding; one is to start to feed, and the other is to change from endogenous to exogenous suitably, or, as mentioned by Kohno *et al.*,[5] to maintain a certain level of feeding.

Acknowledgements

We are grateful to Dr. J. V. Juario and Ms. T. Bagarinao, SEAFDEC Aquaculture Department, for their invaluable advice. For technical assistance, we thank our collegues of Finfish Program, SEAFDEC Aquaculture Department. This study is partially supported by the Japan International Cooperation Agency (JICA).

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