

## Prey selection of hatchery-reared larvae of greater amberjack *Seriola dumerili*

Katsuyuki Hamasaki<sup>1\*</sup>, Ayako Yoshimura<sup>1</sup>, Takashi Iwasaki<sup>2</sup>, Hiroshi Hashimoto<sup>3</sup>, Shigeki Dan<sup>1</sup>

<sup>1</sup>Department of Marine Biosciences, Tokyo University of Marine Science and Technology, Minato, Tokyo 108-8477, Japan. <sup>2</sup>Aquaculture Research Department, Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Ishigaki, Okinawa 907-0451, Japan. <sup>3</sup>Yamaguchi Regional Alliance Office, Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Shimonoseki, Yamaguchi 759-6595, Japan.

\*Corresponding author, e-mail: hamak@kaiyodai.ac.jp

### Abstract

The prey selection of hatchery-reared larvae of greater amberjack *Seriola dumerili* was investigated from 6 to 22 days post-hatching under a co-feeding condition with smaller prey rotifers and larger prey *Artemia*, and the results show that the feeding habits of larvae changed ontogenetically. The prey preference of larvae appeared to shift from rotifers in the preflexion stage, at a < 4.5 mm standard length (SL), through egg-bearing rotifers in the flexion stage, at a > 5 mm SL, to *Artemia* in the postflexion stage, at a > 5.5 mm SL. The majority of larvae with a > 7 mm SL could consume *Artemia*.

**Key words:** *Artemia*; feeding habits; ontogenetic development; prey preference; rotifers

### Introduction

The larvae of many fish species hatch at an early developmental stage and rely on endogenous energy sources (i.e. yolk) for ontogenetic development. They develop eyes and open the mouth, and they then commence exogenous feeding on live prey organisms before complete consumption of endogenous energy reserves (Yúfera and Darias 2007; Hu et al. 2018). Fish larvae can select the prey species on which they prefer to feed, where prey sizes ingested by larvae are correlated with larval body and mouth size in varying degrees depending on species (e.g. Shiota 1970; Anto et al. 2009; Russo et al. 2009; de Lima et al. 2017). Knowledge of the ontogenetic changes in larval feeding habits is therefore crucial to develop an appropriate feeding regimen for successful larval rearing in fish aquaculture.

The greater amberjack *Seriola dumerili* (Risso

1810), belonging to the Carangidae, is a marine pelagic fish species and distributed in warm and tropical waters worldwide. This fish is an important fishery and aquaculture species in Japan and in the Mediterranean region (Tachihara et al. 1993; Nakada 2002; Sicuro and Luzzana 2016; Sley et al. 2016; Corriero et al. 2021). In Japan, greater amberjack aquaculture began in the 1960s and has relied on wild juveniles for seed (Takaoka 2005). Thus, to create a stable aquaculture industry of greater amberjack that does not depend on wild-caught juveniles, it is essential to develop artificial seed production technology, which should lead to the conservation of wild greater amberjack populations.

Live preys used in the seed production of greater amberjack are rotifers *Brachionus plicatilis* species complex and brine shrimp *Artemia* spp. Empirically, small-strain (S-type) rotifers, large-

strain (L-type) rotifers and *Artemia* are supplied sequentially as the larvae grow (Seoka et al. 2000; Shiozawa et al. 2003; Hashimoto et al. 2014, 2015). Hamasaki et al. (2009) elucidated the ontogenetic changes in the prey preferences of greater amberjack larvae from 4 days to 15–20 days post-hatching (dph) by investigating the larval growth and prey size in the guts under a feeding condition with rotifers. The body sizes of rotifers in the larval guts did not vary with larval growth, despite the opportunity for larvae to prey on large size rotifers. Nonetheless, the number of rotifer eggs in the larval guts increased after 12–14 dph, suggesting that larvae appeared to prey selectively on egg-bearing rotifers with larger body sizes. Furthermore, Hashimoto et al. (2015) examined the gut contents of greater amberjack larvae by feeding them with *Artemia* on 13, 16 and 20 dph and revealed that the proportion of larvae ingesting *Artemia* on 13 dph was significantly lower than that on 16 and 20 dph.

Consequently, it can be considered that the feeding habits of greater amberjack larvae change ontogenetically. However, little is known about the prey preferences of greater amberjack larvae under a co-feeding condition with rotifers and *Artemia*. The present study aimed to elucidate the prey selectivity concerning rotifers and *Artemia* of larvae of the greater amberjack as a basis for further improving the knowledge of larval feeding habits during the seed production.

## Materials and Methods

### Larval culture

Larval culture and feeding experiments were conducted from 15 May to 23 June 2008 at the Kamiura Field Station, Japan Fisheries Research and Education Agency, Oita Prefecture, Japan. Eggs were obtained from captive broodstock fish according to the method described by Hamasaki et

al. (2009). In total, ~150,000 buoyant eggs were directly stocked in a 2-kl rectangular tank with still seawater (34 ppt salinity), and after hatching, larvae were subsequently reared in the same tank (cohort 1). Further, ~40,000 larvae at 2 dph that had hatched in a 1-kl cylindrical polyethylene tank were transferred and reared in a 2-kl tank (cohort 2). Larvae were fed with S-type and L-type rotifers and cultured according to the method described by Hashimoto et al. (2015). The larval rearing temperature was controlled at ~25°C using a heater. The photoperiod was 12 h light (6:00–18:00, ~1,000 lx):12 h dark.

### Feeding experiment

Two experiments were conducted to evaluate larval feeding performance. A feeding test was conducted every other day from 6 to 16 dph and on 20 dph in experiment 1 using larvae from cohort 1 and every other day from 6 to 22 dph in experiment 2 using larvae from cohort 2. One and two 100-l polycarbonate tanks containing sand-filtered seawater with aeration via air stones were prepared as test tanks for every test day and seven and 18 tanks in total were used in experiments 1 and 2, respectively.

Prior to initiating the feeding test, ~50 larvae were transferred from a 2-kl rearing tank to each test tank using a small container during the night, at around 19:30, when larvae were inactive and did not feed on prey organisms. On the next morning at around 10:00, a feeding test was initiated by inserting L-type rotifers and *Artemia* into the test tank at 15 and 0.5 individuals/ml, respectively. *Artemia* cysts (Utah Strain) were hatched in one day and incubated for one successive day at 28°C. *Artemia* were then enriched with an enrichment material containing n-3 highly unsaturated fatty acids (Bio-Chromis, Chlorella Industry Co., Ltd., Tokyo, Japan) for 4 h prior to feeding. These

rotifers and *Artemia* were prey organisms used for the seed production of greater amberjack at the Kamiura Field Station. Egg-bearing rotifers occupied the proportions of  $25.3 \pm 8.0\%$  ( $n = 16$ ) of the rotifer populations used for the feeding experiments. Meanwhile, the mean lorica width of non-egg-bearing rotifers and egg-bearing rotifers was 0.17 mm and 0.18 mm, respectively, and the mean total body width of *Artemia* was 0.56 mm. Frequency distributions and mean  $\pm$  standard deviation values of body sizes are detailed for respective prey organisms in Fig. 1.

After feeding times of 15–30 min, ~20 larvae were collected from each test tank and anaesthetised with ethyl 3-aminobenzoate methanesulfonic acid (Sigma-Aldrich Japan K.K., Tokyo, Japan). The SL (notochord length for preflexion larvae) was then measured for 10 specimens using a profile projector (V-12BSC, Nikon Corp., Tokyo, Japan). In experiment 2, the specimens were classified into one of the four ontogenetic stages (i.e. preflexion larvae, flexion larvae, postflexion larvae and juveniles) according to Tachihara et al. (1993). After body size

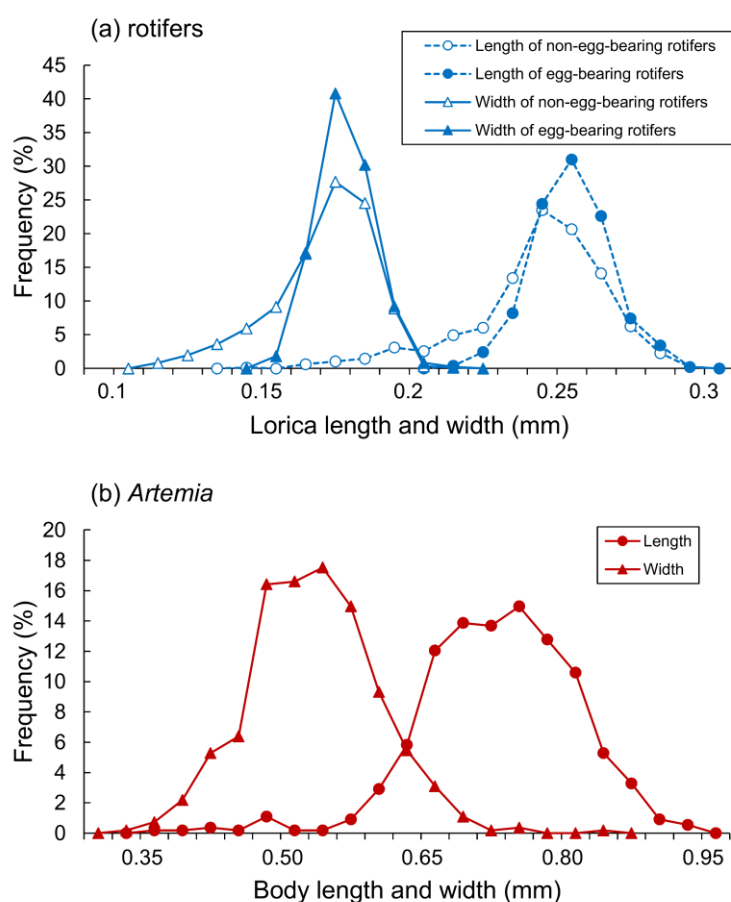


Fig. 1. Size frequency distribution of rotifers (non-egg-bearing rotifers,  $n = 979$ ; egg-bearing rotifers,  $n = 500$ ) (a) and *Artemia* ( $n = 448$ ) (b) used for the feeding experiments of greater amberjack *Seriola dumerili* larvae. The lorica length and width of rotifers and total body length and width of *Artemia*, measured 5–6 times during the larval culture period, are summarized as follows (mean  $\pm$  standard deviation): length of non-egg bearing rotifers ( $0.244 \pm 0.023$  mm), width of non-egg-bearing rotifers ( $0.171 \pm 0.017$  mm), length of egg-bearing rotifers ( $0.255 \pm 0.013$  mm), width of egg-bearing rotifers ( $0.178 \pm 0.009$  mm), length of *Artemia* ( $n = 448$ ,  $0.753 \pm 0.082$  mm) and width of *Artemia* ( $0.558 \pm 0.067$  mm).

measurements, all prey organisms were carefully dissected from the larval guts using fine needles under a stereomicroscope, and the numbers of rotifers and *Artemia* were counted. Rotifer eggs were also counted to infer whether larvae ingested egg-bearing rotifers.

### Feeding performance

Larval feeding performance was evaluated by 1) the incidence [presence (1) or absence (0)] of feeding on rotifers, rotifer eggs (i.e. egg-bearing rotifers) and *Artemia*; 2) prey selectivity of rotifers and *Artemia*; and 3) the rate of consuming each prey item, that is the number of rotifers, rotifer eggs and *Artemia* in the larval guts divided by the feeding time (15–30 min). Prey selectivity of larvae was evaluated using Chesson's selectivity index  $\alpha$  (Chesson 1983):  $\alpha_i = (r_i/p_i) / \sum_1^m (r_i/p_i)$ , where  $r_i$  and  $p_i$  are the proportional abundance of a prey item  $i$  in the gut and the tank in a mixture of  $m$  prey types, respectively. Rotifer eggs could be counted, but it was hard to identify the individual egg-bearing rotifers from the larval guts; therefore, rotifers and *Artemia* were considered prey items in this analysis. The selectivity index for rotifers and *Artemia* was calculated for each individual larva, and it may vary from 0 to 1.

### Statistical analysis

In the present study, the gut contents of larvae were examined using 10 specimens collected from the same test tank, and this was repeated at different larval ages. A binomial generalised linear mixed effects model (GLMM) was therefore employed to evaluate the effects of larval growth (SL) on the incidence of feeding on each prey item or prey selectivity (Chesson's selectivity index) of *Artemia*, while considering pseudo-replications of the data (Zurr et al. 2009). A linear mixed effects model (LMM) was also conducted to evaluate the

larval prey consumption rate. This analysis of rotifer eggs and *Artemia* was conducted for larvae with  $\geq 5$  mm and a  $\geq 5.5$ -mm SL, respectively, due to the little amount of these prey items in the guts of smaller larvae. In the GLMM and LMM analyses, identical numbers of test tanks (experiment 1) and of test tanks and larval ages (dph) (experiment 2) were included as random intercept effects. Statistical analyses were performed using the R statistical software (R4.2.1; R Core Team 2022) at a 5 % significance level. The binomial GLMM analysis was run using the *glmer* function (logit link) implemented in the lme4 package (Bates et al. 2015), and the LMM analysis was conducted using the *lmer* function in the lme4 and lmerTest packages (Kuznetsova et al. 2017).

### Results

The mean SL value of larvae linearly increased from 3.9 mm to 8 mm during the larval culture periods (Fig. 2a). Ontogenetic stages progressed in accordance with age and growth, as follows (main dph and SL class) (Fig. 2b, c): preflexion larvae, 6–10 dph and 3.5–4.5 mm; flexion larvae, 10–16 dph and 4–6 mm; postflexion larvae, 16–22 dph and 5.5–9 mm; and juveniles, 22 dph and 8.5–9.5 mm.

A similar larval feeding performance was observed in both experiments (Fig. 3). Further, larval body size had significant positive effects on the feeding incidence, selectivity index and consumption rate of respective prey organisms ( $p = < 0.0001$ – $0.0273$ ), except for the incidence of feeding on rotifers in both experiments and the rate of consuming rotifer eggs in experiment 1; however, the larval body size tended to affect these larval feeding performances positively ( $p = 0.0606$ – $0.0850$ ) (Table 1). The feeding incidence for each prey organism and the selectivity index for *Artemia* increased when increasing SL (Fig. 3a–d), and the feeding incidence shifted from rotifers

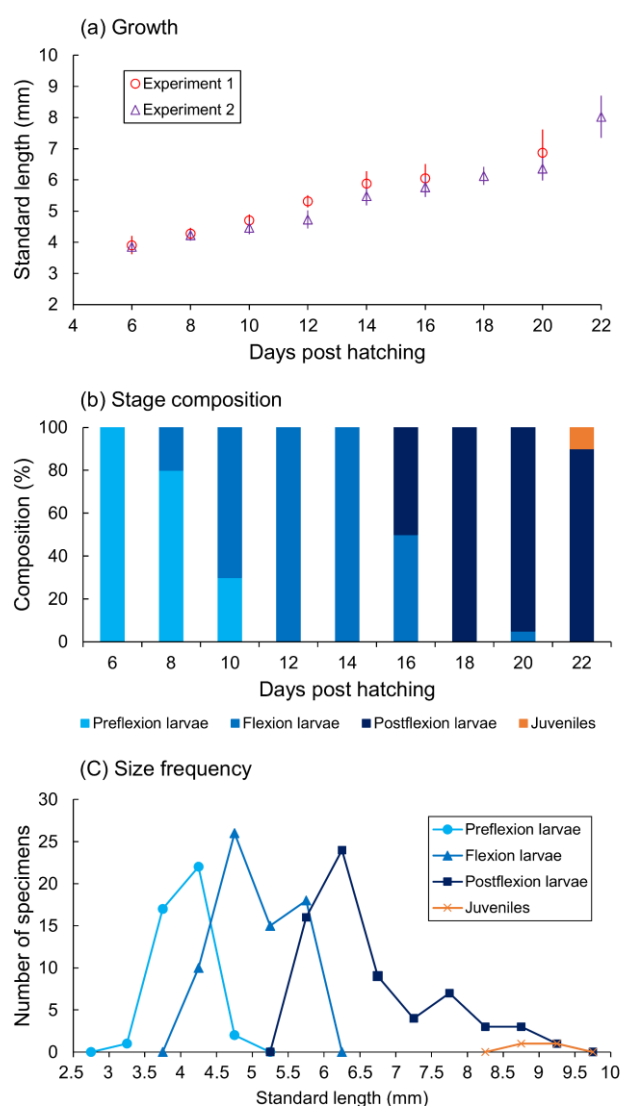


Fig. 2. Growth and ontogenetic stage compositions in relation to age (days post-hatching) and size frequency distributions in respective ontogenetic stages (preflexion larvae, flexion larvae, postflexion larvae and juveniles) during the larviculture of greater amberjack *Seriola dumerili*.

through egg-bearing rotifers to *Artemia* (Fig. 3a, b). The rotifer consumption rate linearly increased with an increasing SL, and rotifer egg and *Artemia* consumption rates linearly increased after growing to 5 mm and a 5.5-mm SL, respectively (Fig. 3e, f).

## Discussion

The present study demonstrated that the feeding habits of greater amberjack larvae changed ontogenetically under a co-feeding condition with

rotifers and *Artemia*. Prey preference of larvae appeared to shift from rotifers in the preflexion stage, at a < 4.5-mm SL, through to egg-bearing rotifers in the flexion stage, at a > 5-mm SL, and to *Artemia* in the postflexion stage, at a > 5.5-mm SL. It has been reported that the amount of prey in the guts of greater amberjack larvae increased after a 4.5-mm SL, especially a > 5 mm-SL for rotifer eggs (Hamasaki et al. 2009) and after a ~6-mm total length (TL) ( $\approx$  5.5-mm SL) for *Artemia* (Hashimoto et al. 2015), which is consistent with observations in the present study.

The morphological and physiological development of greater amberjack larvae is likely related to their ontogenetic shift in the prey selectivity. For example, the proportions of head length, upper jaw length, eye diameter, body height and TL to SL increased during the flexion and postflexion stages (Tachihara et al. 1993; Seoka et al. 2000; Hamasaki et al. 2009). The rudiments of ventral, dorsal and anal fins began to develop, and the vertebra was well ossified during the postflexion stage (Tachihara et al. 1993), while pepsin-like enzyme activity increased after the flexion stage (Seoka et al. 2000).

Hamasaki et al. (2009) documented that greater amberjack larvae consumed rotifers with similar body sizes from ~3.5 mm SL (mouth opening) to ~7.6 mm SL, and larvae preyed on smaller-size classes of rotifer populations in the tanks. The feeding habits of greater amberjack larvae in the tanks may reflect those of larvae in nature. Although the gut contents of wild larvae have not been documented for greater amberjack, they may prey on copepods, which are important prey organisms for fish larvae in nature (Chesney 2005). It has been reported that the larvae of the wild Atlantic mackerel, *Scomber scombrus* Linnaeus 1758 (Scombridae), exhibited feeding

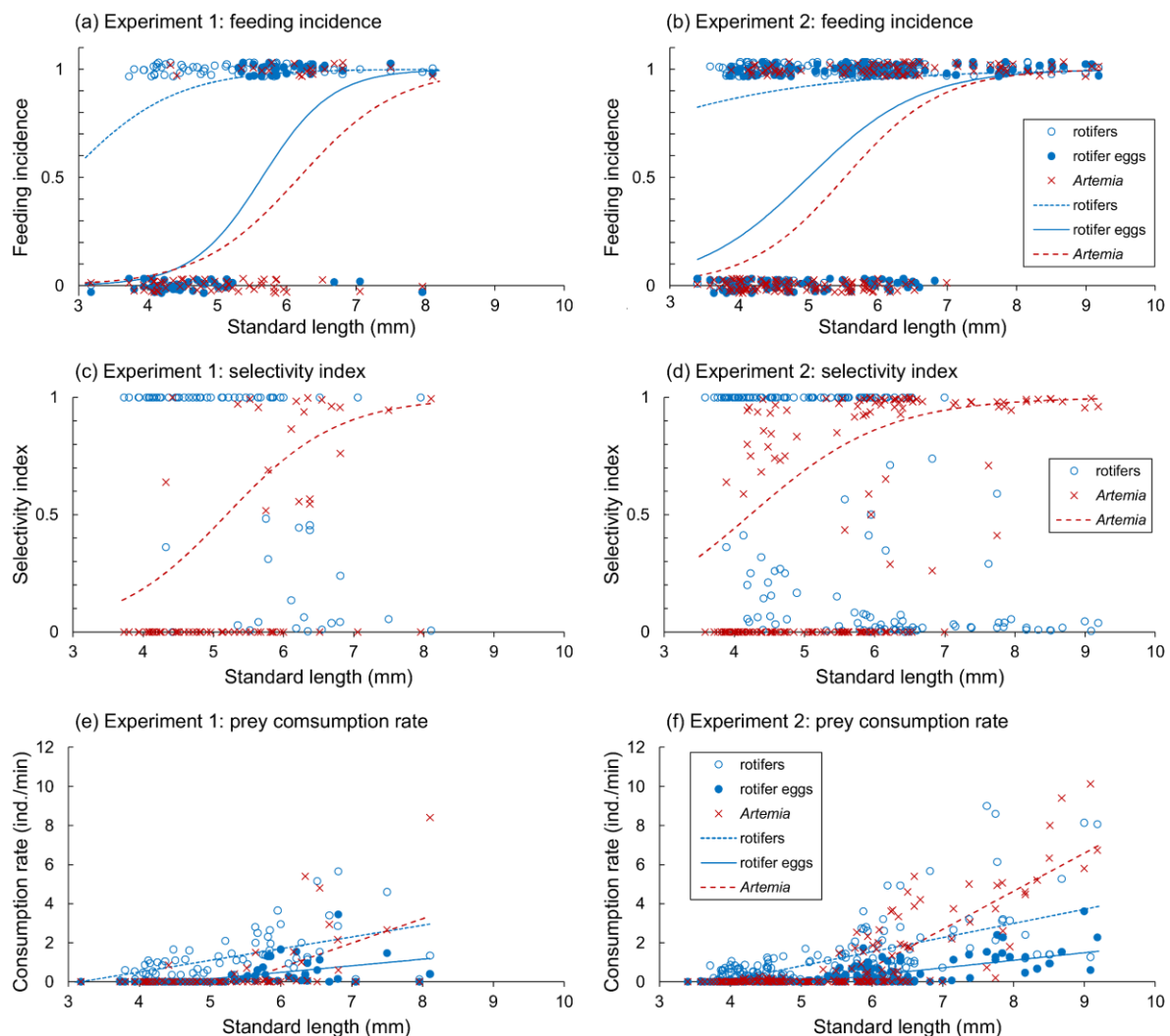


Fig. 3. Relationships between SL and incidence [presence (1) or absence (0)] of feeding on rotifers, rotifer eggs and *Artemia* (a, b); Chesson's selectivity index for rotifers and *Artemia* (c, d), and rate of consumption of rotifers, rotifer eggs and *Artemia* (e, f) in individual larvae of greater amberjack *Seriola dumerili*. Two experiments were conducted using different cohort larvae. Data on feeding incidence are randomly scattered around 1 or 0 for clarity. Curves and lines were drawn based on the coefficient estimates of the GLMM or LMM for evaluating the larval feeding performance, which is summarized in Table 1.

habits similar to the laboratory-reared larvae of greater amberjack. The scatter plots of prey widths eaten by mackerel larvae against the fish length indicated that larvae of a 3.5–8-mm TL selected prey (nauplii stage III–V of copepods) of similar widths of  $< \sim 0.2$  mm, but larvae of a  $> 6.5$ -mm TL ate increasingly larger prey (nauplius stage VI, copepodites and then other mackerel larvae) of a  $\sim 0.2$ –0.8-mm width (Peterson and Ausubel 1984).

In the later phase of the seed production of greater amberjack, mass mortality often occurs due

to the injury and death of smaller larvae and juveniles caused by the aggressive behaviour and cannibalism of larger juveniles, and the size heterogeneity of cultured larvae and juveniles is strongly associated with the degrees of aggressive behaviour and cannibalism (Miki et al. 2011; Hashimoto et al. 2014). Fish mortality due to aggression and cannibalism also occurs during the larviculture of *Seriola* species, such as *S. quinqueradiata* Temminck et Schlegel 1845 (Sakakura and Tsukamoto 1996) and *S. lalandi*



Table 1. Relationship between standard length (SL) and feeding performance in larvae of greater amberjack *Seriola dumerili*. Two experiments were conducted using different cohort larvae. A binomial generalised linear mixed effects model (GLMM) was applied to evaluate the incidence [presence (1) or absence (0)] of feeding on rotifers, rotifer eggs and *Artemia* and Chesson's selectivity index for *Artemia*. A linear mixed effects model (LMM) was used to evaluate the rate of consumption of respective prey (individuals/min).

Response variable	Exp.	Prey	n	Coefficient	Estimate	Std. error	z or t values	p
Feeding incidence	1	rotifers	70	Intercept	-3.6403	3.0960	-1.176	0.2397
				SL	1.2936	0.6895	1.876	0.0606
		rotifer eggs	70	Intercept	-11.2220	4.8100	-2.333	0.0196
				SL	1.9880	0.9010	2.207	0.0273
		<i>Artemia</i>	70	Intercept	-8.6466	2.1980	-3.934	0.0001
				SL	1.3988	0.3828	3.654	0.0003
	2	rotifers	180	Intercept	-0.4291	1.7066	-0.251	0.8010
				SL	0.5817	0.3377	1.722	0.0850
		rotifer eggs	180	Intercept	-6.1990	1.9210	-3.227	0.0013
				SL	1.2400	0.3620	3.425	0.0006
		<i>Artemia</i>	180	Intercept	-7.9640	2.0650	-3.856	0.0001
				SL	1.4420	0.3840	3.755	0.0002
Selectivity index	1	<i>Artemia</i>	66	Intercept	-6.4929	2.5272	-2.569	0.0102
				SL	1.2513	0.4501	2.780	0.0054
	2	<i>Artemia</i>	167	Intercept	-4.3502	1.4591	-2.981	0.0029
				SL	1.0292	0.2541	4.051	< 0.0001
Consumption rate	1	rotifers	66	Intercept	-1.8922	0.9476	11.120	0.0709
				SL	0.5982	0.1743	11.343	0.0054
		rotifer eggs	39	Intercept	-1.5223	1.1249	19.310	0.1916
				SL	0.3346	0.1837	20.624	0.0831
		<i>Artemia</i>	32	Intercept	-6.7770	2.9452	18.035	0.0335
				SL	1.2509	0.4706	17.997	0.0160
	2	rotifers	167	Intercept	-2.8128	0.6377	-4.411	0.0014
				SL	0.7255	0.1131	6.417	0.0001
		rotifer eggs	98	Intercept	-1.9940	0.5479	-3.639	0.0026
				SL	0.3867	0.0849	4.553	0.0004
		<i>Artemia</i>	86	Intercept	-10.9688	1.6639	-6.592	< 0.0001
				SL	1.9513	0.2537	7.691	< 0.0001

Valenciennes 1833 (Ebisu and Tachihara 1993; Moran 2007). Moran (2007) reported that the body size variability increased substantially from 12 dph when *Artemia* feeding was initiated in the seed production of *S. lalandi*. Meanwhile, Hashimoto et al. (2015) examined the effect of an *Artemia* feeding schedule on size heterogeneity in greater

amberjack seed production. Variations in body size at 25 dph were negatively correlated with fish ages (i.e. 13, 16 and 20 dph) at the initiation of *Artemia* feeding. Yet, larvae that successfully prey on *Artemia* are considered to grow at a faster rate, resulting in increased size heterogeneity in tanks supplemented with *Artemia* at an earlier stage,

before all fish are able to consume large prey.

In the present study, some flexion and preflexion larvae positively selected *Artemia*, and most postflexion larvae with a > 6.5-mm SL preyed on *Artemia*. Consequently, it can be recommended that *Artemia* supplementation should begin when most cultured larvae exceed a 6.5-mm SL to reduce the size heterogeneity that causes mass mortality due to aggressive behaviour and cannibalism by juveniles in greater amberjack seed production.

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