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Influence of temperature on yolk resorption in common snook *Centropomus undecimalis* (Bloch, 1792) larvae

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Abstract

To determine the optimal rearing temperature for *Centropomus undecimalis* larvae during the yolk resorption period, changes in larval development were measured at four different temperatures (23, 25, 28 and 31°C). Yolk and oil-globule volume was recorded for 25 larvae at four different times. This involved an initial measurement at hatch and at 24, 48 and 72 h posthatch (hph). Additional morphological measurements included standard length, body height and eye diameter. On average, at the end of the three trials, larvae reared at 25°C had a longer mean standard length than larvae reared at 23, 28 and 31°C. Larvae reared at 25°C also had more yolk and oil globule reserves than larvae raised at 28 and 31°C. The body height:length residuals were also the highest at 25°C (i.e. larvae had deeper or stockier bodies). The yolk sac was present up to 72 hph at 23 and 25°C, while it was entirely consumed after 48 hph in larvae held at 28 and 31°C. Larvae showed the fastest growth during the first 24 hph in all temperature treatments; this period corresponded to the highest energy consumption as determined by the decrease in yolk sac and oil-globule volume. Eye diameter did not vary significantly with time during yolk-resorption. We conclude that a temperature near 25°C is optimal for raising snook larvae during the yolk-resorption period.

Keywords: snook, larval development, ontogeny, growth, aquaculture

Introduction

The common snook, *Centropomus undecimalis*, is distributed in tropical and subtropical rivers, estuaries and oceanic habitats of North and South America (Rivas 1986; Alvarez-Lajonchère & Tsuzuki 2008). Common snook have become a high priority species for conservation and aquaculture because they are both ecologically and economically important (Winner, Blewett, McMichael & Guenther 2010). Along the Gulf Coast of the United States, common snook are part of a popular recreational fishery. However, factors such as environmental change (kills due to episodes of extreme cold), habitat destruction and overfishing have led to concerns among resource managers (Muller & Taylor 2012). Advances in aquaculture technologies are being developed to increase the production of common snook fingerlings for stock enhancement as a fisheries management tool (Brennan, Leber, Blankenship, Ransier & DeBruler 2005; Brennan, Walters & Leber 2008). Additional interests include the development of commercial scale aquaculture production techniques in South America and Mexico where the common snook is a popular staple food (Alvarez-Lajonchère & Tsuzuki 2008).

Since 1996, Mote Marine Laboratory and the Florida Fish and Wildlife Conservation Commission have conducted joint research to enhance snook stocks and to develop aquaculture technologies to produce fingerlings for release (Brennan *et al.* 2005). In 2006, maturation and spawning of

captive snook broodstock was achieved at Mote's Center for Aquaculture Research and Development. Research has since focused on improving captive broodstock spawning (Rhody, Neidig, Grier, Main & Migaud 2013) and larval rearing capabilities (Wittenrich, Rhody, Turingan & Main 2009; Rhody, Nassif & Main 2010; Yanes-Roca & Main 2012; Yanes-Roca, Rhody, Nystrom, Wittenrich & Main 2012). To date, larval mortality remains one of the bottlenecks in snook aquaculture. A number of obstacles must still be resolved to achieve large scale production of fingerlings. These include defining the optimal conditions for efficient use of limited yolk reserves, understanding live food requirements and determining optimal timing for introducing prey items as the larvae transition from endogenous to exogenous feeding.

In both cultured and wild marine fish species, there is high mortality prior to the full transition from endogenous to exogenous active feeding (Jaworski & Kamler 2002; Yufera & Darias 2007; Jaroszewska & Debrowski 2011); estimating mortality rates during this period is an important index of recruitment success. Changes in morphometry can also be used as indices of both tissue mobilization and yolk utilization rate in larval development studies. Changes in standard length (SL) during the period of endogenous feeding have been successfully used as a relative measure of yolk conversion efficiency in red snapper *Lutjanus campechanus* (Williams, Papanikos, Phelps & Shardo 2004) and summer flounder *Paralichthys dentatus* (Watanabe, Feeley, Ellis & Ellis 1998). According to a review by Wiegand (1996) on utilization of yolk lipids by teleost fish, critical processes during early development are the rate and efficiency of yolk-sac resorption and the allocation of yolk for embryo development and metabolic energy. Temperature controls the efficiency at which yolk is converted into body tissue (Kamler 2008) and affects the size of larvae at first feeding and the time between hatching and starvation (Hunter 1981). Higher than optimal temperatures can result in embryos that develop faster (Das, Pal, Chakraborty, Manush, Dalvi, Sarma & Mukherjee 2006) and lower than optimal temperatures typically yield slower growing larvae (Small & Bates 2001). Suboptimal temperatures can lead to an increased incidence of deformity and higher mortality rates (Houde 1974).

Clearly, identifying optimum environmental rearing conditions for individual species is an important aspect of aquaculture research. The optimal temperature for the development of *C. undecimalis* larvae during the yolk resorption period has not yet been defined. The research presented here examines the influence of temperature during the first few days of the larval development. The approach was to conduct morphometric measurements of *C. undecimalis* larvae exposed to different temperature treatments under controlled laboratory conditions.

Materials and methods

Broodstock

Centropomus undecimalis eggs and sperm were obtained from captive broodstock maintained in 48 m^3 circular tanks at the Mote Aquaculture Research Park in Sarasota, Florida. Each broodstock system consisted of a 4.57 m diameter fibreglass tank with a total system volume of 28 m^3. A temperature of 28°C (±1°C) was maintained in each tank by cycling water through an individual heater/chiller unit (AquaCal Autopilot, St. Petersburg, FL). The filtration system included a 0.085 m^3 drop filter, 900-L moving bed for bio-filtration, protein skimmer and an ultraviolet light (UV) sterilization unit. Salinities were maintained at 35 (±1). In July 2010, September 2010 and March 2011, snook broodstock were strip-spawned following induction with gonadotropin-releasing hormone (GnRHa) according to methods described in Rhody *et al.* (2013). Milt was collected using a syringe and cannula and then stored on ice, whereas eggs were stripped from female snook. Eggs were fertilized with milt from several males; sperm was activated with sea water with a salinity of 35.

Experimental design

Three rearing experiments were conducted using three separate batches of eggs that came from different females and a pool of sperm from several males, to test larval development at different temperatures. Each of the three experiments consisted of 25 microcosms per temperature treatment set in shallow rectangular raceways supplied with recirculating water and exposed to UV filtration. The raceway allowed water to flow around and under each microcosm. The microcosms were small PVC cylinders 2.6 cm in diameter. The base of each

microcosm was covered with a 95 μm nitex nylon mesh to prevent escape of larvae and to allow circulation of water (operational volume 330 mL^{-1}). The top of the microcosm extended above the surface of the water bath and was exposed to air. The microcosms were placed on an elevated platform randomly distributed within the raceway.

Eggs were transferred immediately after fertilization into 10 L aerated hatching tanks (28°C). At 4–6 h post fertilization (blastula stage), aeration was removed and nonviable eggs (i.e. those that sank to the bottom of the tank) were discarded. In the first two experiments, floating eggs (n = 200) were transferred from the 10 L hatching tanks into individual microcosms (n = 25) located in temperature-controlled raceways. Water in the raceways was maintained at 28°C at the time of transfer and until larvae hatched, approximately 17 h postfertilization. After hatching, raceway water temperatures were adjusted over a 6 h period until target treatment temperatures were achieved (25, 28 and 31°C). In all trials, temperatures were then maintained by setting the room air conditioning unit to a lower temperature and then heating the raceways to 25, 28 and 31°C, plus a fourth temperature of 23°C for the third trial, using heaters with thermostats. To track temperature stability and accuracy (±0.5°C), temperature was recorded every 15 min by data loggers (Hobo Data Logger; Onset Computer Corporation, Bourne, MA, USA) immersed in each raceway. Treatment temperatures were selected based on preliminary research identifying 28°C as the optimal temperature for egg incubation (Yanes-Roca & Main 2012; Yanes-Roca, Rhody *et al.* 2012).

For the third experiment, eggs obtained from a single broodstock mass spawning event (Rhody *et al.* 2013) were transferred from the broodstock tank (28°C) to 10 L hatching tanks (28°C). The rearing microcosms were stocked with newly hatched larvae (9 h posthatch) and stocking density was 200 larvae per microcosm. Raceway tanks were adjusted to the appropriate water treatment temperatures as described above. In addition to treatments at 25, 28 and 31°C, a 23°C treatment was added to examine response of the larvae to a lower temperature. Larvae instead of eggs were used in this experiment. This minimized the impact of vigorous bacterial growth on larvae that was observed in the first two trials. Rapid bacterial growth was presumed to be from decay of materials associated with egg hatch.

Parameters measured and statistical analyses

Larval development was monitored at four times: hatching, 24 h posthatch (hph), 48 hph, and 72 hph. Approximately 25 individuals from each system were removed at each time point. Sampled larvae were mounted in a Sedgewick-Rafter counting slide and photographed using a compound microscope fitted with a digital camera. Measurements were conducted using the photomicrographs. Specific measurements included SL, body height at anal pore, eye diameter, yolk sac length and height, and oil globule diameter. These metrics were extracted using Visilog 6.8 software (Noesis, Saint Aubin, France). Yolk-sac volume was calculated using the formula for a prolate spheroid $V = 4/3\ \pi lh^2$, where l is yolk-sac length and h is yolk-sac height.

We used the nonparametric Kruskal–Wallis ANOVA to identify significant ($P < 0.05$) temperature-related variations in median morphological measurements and used the nonparametric Mann–Whitney test for two-sample comparisons. Best-fitting regression models were identified to describe the empirical relationship between yolk and oil-globule consumption and temperature.

Results

The first trial lasted only 48 hph. At 72 hph, there were too few larvae available to collect meaningful observations. There were no data available for the 31°C treatment at 48 hph because all larvae in this group had died.

Among the morphological parameters measured, SL, yolk volume and oil-globule volume had the most consistent relationships with temperature. Eye diameter did not vary significantly with time. Other potential condition indicators include various ratios of morphological measurements. Among these ratios, body height:length increased with body length (SL), yet the relationship with SL explained only 20% of the variation in height:length (linear regression, n = 595, R^2 = 0.20, slope $P < 0.0001$). The residuals from this regression, which were distributed evenly above and below the regression line, were examined as a potential condition indicator. They varied significantly with temperature (Kruskal–Wallis test, P = 0.003). Larvae raised at 25°C had higher residual height:length (deeper bodies) than larvae raised at 28 or 31°C (Mann–Whitney tests,

$P < 0.002$). The larvae raised at 23°C had the second-highest residual height:length, but this was not statistically different from larvae at other temperatures.

Initial measurements of morphological parameters (hph = 0) were significantly different among trials (Kruskal–Wallis ANOVA, $P < 0.05$) therefore, we converted measurements of SL, yolk volume and oil-globule volume to percentages, setting initial values (hph = 0) at 100% for each trial (Table 1).

Percent standard length

During the first trial, larvae in the 25°C treatment had higher median percent SL (Table 1). The second trial was conducted to 72 hph, and larvae at 25°C again had the highest percent SL (Fig. 1). Even though all treatments reached 72 hph in the second trial, most larvae in the 31°C treatment died by the conclusion of this sampling interval, making it difficult to obtain the 25 larvae needed for comparison. Larvae in the third trial once again had the highest percent SL at 25°C, and larvae in the 31°C treatment died after 48 hph. Given the trend of increasing percent SL at lower temperatures that was evident in the first two trials, a lower temperature, 23°C, was added to the third trial. However, lowering water temperature to 23°C did not improve percent SL. The greatest increase in percent SL occurred during the first 24 hph; there was very little growth afterwards (Table 1).

Yolk volume

Rapid consumption of yolk occurred during the first 24 h after hatching (Table 1). During this time, larvae used 87–98% of their yolk, and the percentage consumed increased with temperature (i.e. regression slopes are more negative at higher temperatures; Fig. 2). Even though the percentage of yolk consumed varied from one treatment to another, all treatments consistently showed most of the yolk being absorbed in the first 24 hph. At the ends of trials 2 and 3, larvae at higher temperatures had completely depleted their yolk supplies (Table 1).

Oil-globule volume

The highest consumption of the oil globule also occurred during the first 24 hph. However, the percentage consumed was not as high as that of yolk. During this period, larvae utilized 53–77% of their oil globule reserves. At the end of the first trial (48 hph) larvae at 25 and 28°C had some oil globule remaining, while those at higher temperatures and in the longer (72 hph) second and third trials had depleted their oil globules. As with yolk, empirical regressions describing the decrease (as percent) in remaining oil globule had high levels of fit. The median percentage consumed increased with temperature (regression slopes were more negative at higher temperatures):

23°C	Percent = 99.8 – 11.6*sqrt(hph); ($n = 4$, $R^2 = 0.99$, $P = 0.003$)
25°C	Percent = 98.1 – 12.0*sqrt(hph); ($n = 11$, $R^2 = 0.98$, $P < 0.0001$)
28°C	Percent = 96.9 – 12.3*sqrt(hph); ($n = 11$, $R^2 = 0.98$, $P < 0.0001$)
31°C	Percent = 97.1 – 12.9*sqrt(hph); ($n = 9$, $R^2 = 0.98$, $P < 0.0001$)

Discussion

Temperature regulates the metabolic requirements for food and the rates of food processing (Brett & Groves 1979), food intake and growth (Peter 1979). A rise in temperature of 10°C typically increases the metabolic rate by a factor of about 2.3 (Brett & Groves 1979). Therefore, when temperature increases, the rates of metabolic requirements also increase (Blaxter & Hempel 1966). Similarly, the energy available in the yolk-sac and oil globule is used to support growth of new tissue, for larval development and for basic body functions (Gray 1926).

The optimal temperature for development and growth during different life stages of fish varies with environmental conditions (Gadomski & Caddell 1991; Imsland, Sunde, Folkvord & Stefansson 1996). Yanes-Roca and Main (2012) found the highest hatching rate for *C. undecimalis* at 28°C. Stephen and Shafland (1982) reported that newly hatched larvae incubated at 28°C measured 1.4–1.5 mm SL, which is within the range we found in our study (1.3–1.7 mm). Broodstock variability is another factor known to be critical for egg quality (Yanes-Roca *et al.* 2009; Kjorsvik, Mangor-Jensen & Holmefjoerd 1990). Differences in broodstock may have been responsible for the variation in initial characteristics of recently hatched larvae in our experiments. We accounted for these

Table 1 Median larval snook standard length, yolk volume and oil-globule volume, with probability values (KW *p*) from Kruskal–Wallis tests of temperature effects (Temp), where NS indicates KW $P > 0.05$. Time is hours posthatching (hph) and *n* is number of individual larvae contributing to median determinations, which were converted to percentages to offset incipient (broodstock-related) morphometric differences. Within each trial and time combination, X is vertically aligned if Mann–Whitney tests indicated temperature comparisons were not statistically different ($P > 0.05$). Trial 1 and 2 larvae were hatched within test microcosms. Trial 3 larvae were transferred to test microcosms from a common source; initial measurements (hph = 0) in trial 3 describe the common source

			Standard length					Yolk volume					Oil-globule volume				
Trial	Time (hph)	Temp (°C)	*n*	Median (mm)	Percent	KW *p*		*n*	Median (mm^3)	Percent	KW *p*		*n*	Median (mm^3)	Percent	KW *p*	
1	0	25	25	1.57	100.00	–		25	0.811	100.00	–		25	0.0042	100.00	–	
		28	25	1.68	100.00			25	0.749	100.00			25	0.0036	100.00		
		31	25	1.65	100.00			25	0.764	100.00			25	0.0036	100.00		
	24	25	25	2.45	156.05	0.0001	X	25	0.027	3.29	<0.0001	X	25	0.0010	24.41	NS	
		28	25	2.44	145.24		X	25	0.028	3.71		X	25	0.0009	25.19		
		31	25	1.92	116.36		X	25	0.038	4.95		X	25	0.0012	32.03		
	48	25	24	2.52	160.51	<0.0001	X	23	0.014	1.72	NS		23	0.0005	12.50	NS	
		28	25	2.28	135.71		X	25	0.013	1.75			25	0.0004	10.63		
2	0	25	25	1.33	100.00	–		25	0.861	100.00	–		25	0.0031	100.00	–	
		28	25	1.37	100.00			25	0.835	100.00			25	0.0031	100.00		
		31	25	1.42	100.00			25	0.871	100.00			25	0.0031	100.00		
	24	25	25	2.55	191.73	0.0007	X	25	0.048	5.62	<0.0001	X	25	0.0014	47.05	<0.0001	X
		28	24	2.45	178.83		X	24	0.030	3.60		X	24	0.0009	29.63		X
		31	25	2.36	166.20		X	25	0.021	2.46		X	25	0.0007	22.82		X
	48	25	22	2.56	192.11	0.01	X	22	0.014	1.64	<0.0001	X	21	0.0005	17.15	<0.0001	X
		28	21	2.40	175.18		X	21	0.009	1.10		X	21	0.0003	8.78		X
		31	24	2.42	170.42		X	24	0.006	0.73		X	24	0.0003	8.78		X
	72	25	24	2.56	192.11	NS		24	0.005	0.59	<0.0001	X	25	0.0001	2.14	<0.0001	X
		28	22	2.49	181.39			21	0.000	0.00		X	21	0.0000	0.00		X
		31	23	2.48	174.65			24	0.000	0.00		X	24	0.0000	0.00		X
3	0	23	25	2.26	100.00	–		25	0.243	100.00	–		25	0.0026	100.00	–	
		25	25	2.26	100.00			25	0.243	100.00			25	0.0026	100.00		
		28	25	2.26	100.00			25	0.243	100.00			25	0.0026	100.00		
		31	25	2.26	100.00			25	0.243	100.00			25	0.0026	100.00		
	24	23	25	2.32	102.65	NS		25	0.027	10.96	0.01	XX	25	0.0012	44.72	0.03	X
		25	25	2.39	105.75			25	0.033	13.40		X	25	0.0009	35.17		XX
		28	25	2.36	104.42			25	0.027	10.96		XX	25	0.0009	35.17		XX
		31	25	2.35	103.98			25	0.024	9.71		X	25	0.0007	27.09		X
	48	23	25	2.23	98.67	0.003	X	25	0.011	4.37	<0.0001	X	25	0.0004	14.84	0.001	X
		25	25	2.40	106.19		X	25	0.010	4.05		X	25	0.0003	10.42		X
		28	24	2.33	102.88		X	24	0.007	2.98		X	24	0.0003	10.42		XX
		31	25	2.39	105.75		X	25	0.005	2.07		X	25	0.0002	6.98		X

Table 1 (continued)

			Standard length					Yolk volume					Oil-globule volume				
Trial	Time (hph)	Temp (°C)	*n*	Median (mm)	Percent	KW *p*		*n*	Median (mm^3)	Percent	KW *p*		*n*	Median (mm^3)	Percent	KW *p*	
	72	23	24	2.32	102.43	0.004	X	24	0.003	1.36	<0.0001	X	24	0.0001	4.40	<0.0001	X
		25	24	2.44	107.74		X	24	0.000	0.00		X	24	0.0000	1.30		X
		28	15	2.13	94.25		X	15	0.000	0.00		X	15	0.0000	0.00		X

differences by normalizing our observations to initial measurements (i.e. we report percent changes relative to initial characteristics).

Our experiments show that larvae at 25°C had greater SL at the end of each of the three trials than larvae grown at other temperatures (Table 1). They were also more likely to retain energy reserves after 48 h than larvae raised at higher temperatures (Fig. 3). Our results show optimal growth of *C. undecimalis* larvae occurred at 25°C. Also, larvae needed less energy to satisfy their metabolic demands, allowing energy for conversion into new tissue. Larvae raised at 23°C exhibited a variety of malformations, but had relatively large amounts of energy remaining at the end of the trial (Fig. 3). This suggested a negative influence on early larval development, reduced metabolic rate and low energy consumption at 23°C. These larvae were not likely to be viable, and we concluded that this incubation temperature was not ideal under aquaculture conditions. In our study, larvae at 28°C exhausted their energy supplies before those at 25°C, and they grew more slowly. The larvae in the 28°C treatment appeared to use energy more efficiently than larvae at 23°C, yet they would likely have lower survival rates unless they were able to capture prey earlier than larvae reared at lower temperatures. Finally, the increased metabolic requirements of larvae grown at 31°C led to premature exhaustion of their energy reserves and an early death by starvation compared to larvae at lower temperature treatments. Even though larvae at 31°C reached the 72 hph during the second trial, it was difficult to obtain the 25 larvae sample because very few larvae were remained alive. Based on the early mortality of these larvae, we concluded that 31°C was not an optimal temperature to raise snook larvae during the yolk resorption period.

Fish, as in all poikilotherms, have an optimal temperature for growth and survival (Brett & Groves 1979; Gadomski & Caddell 1991). Marine fish larvae tend to increase protein catabolism after yolk-sac resources become depleted (Wright & Fyhn 2001). Williams *et al.* (2004) suggested that this may help larvae to digest their first prey, but they also suggested that if a significant portion of proteins used for metabolic needs arises from tissue resorption, this will reduce larval length prior to first feeding. Fully developed larvae, (in terms of standard length, pigmented eyes, open mouth and

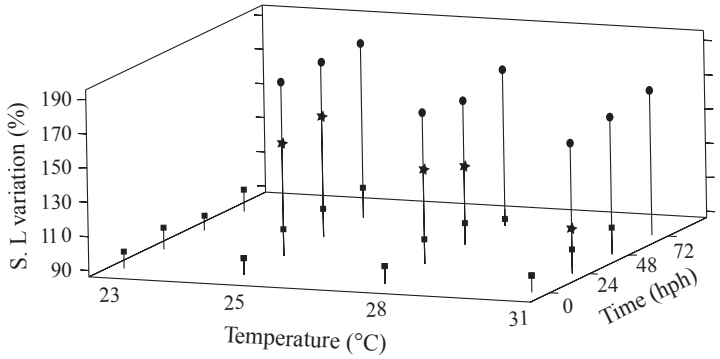

Figure 1 Standard length variation (%) for different temperature treatments at different hours posthatching (hph). Trials one, two and three are shown with stars, circles and squares symbols respectively.

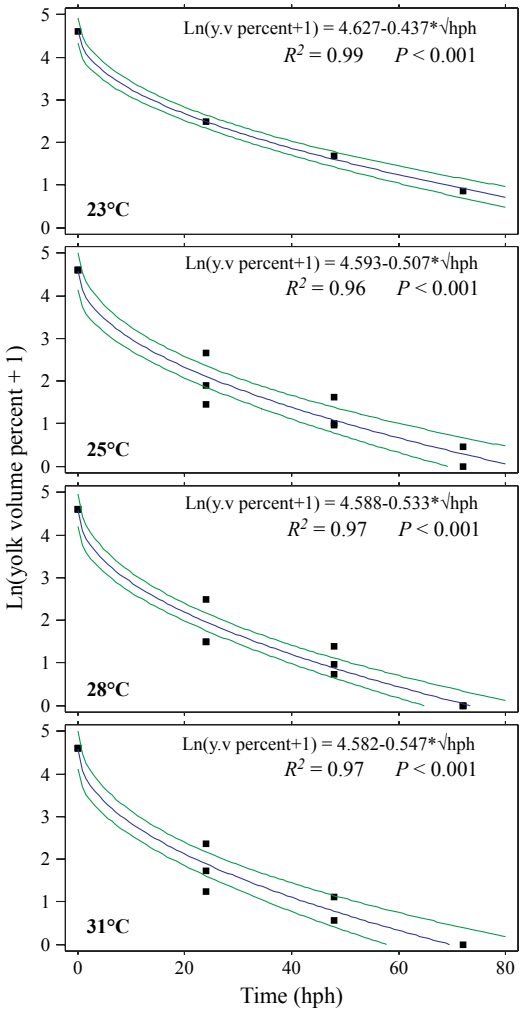

Figure 2 Yolk depletion in the four temperature treatment. Temperature of each treatment is indicated at the bottom of each panel. Green lines indicate 95% confidence intervals.

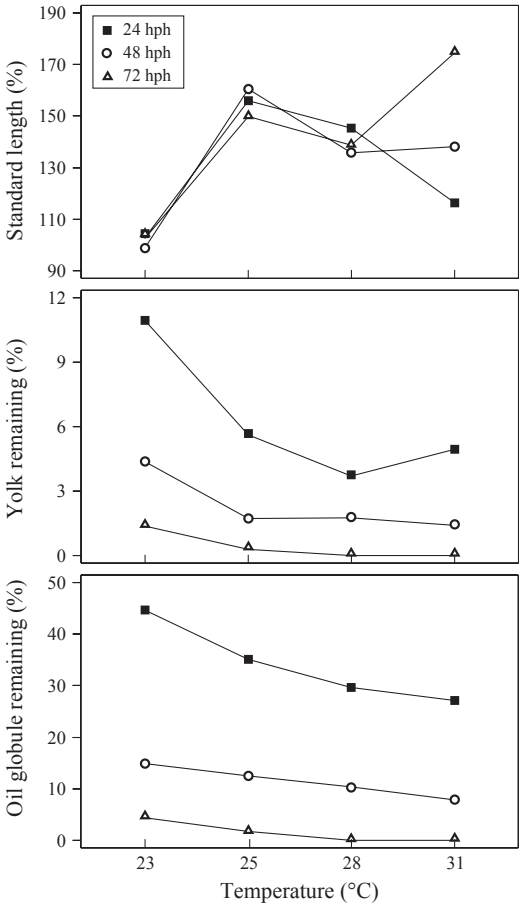

Figure 3 Percent standard length, percent yolk remaining and percent oil globule remaining for larvae grown in the four temperature treatments and at different hours posthatching (hph).

anal pore) with additional energy reserves may either use surplus energy to pursue prey directly or use the energy to grow further, gaining an

advantage when later pursuing their first prey. Our results demonstrate that 25°C was the optimal temperature for raising snook larvae during this specific period of their life cycle. This is consistent with previous observations that many fish tend to live longer and grow larger in the cooler part of their temperature range (Ricker 1979).

Embryos and larvae must subsist on yolk and oil reserves until their digestive and feeding systems develop sufficiently for prey capture and digestion (Green & McCormick 2001). Further studies of the development of the digestive system of snook larvae at 25 and 28°C would help determine when they may be ready for first feeding and whether raising larvae at 25°C enhances fish recruitment and a healthy population. Due to the rapid metamorphosis process in *C. undecimalis* larvae, such studies could be conducted examining shorter time frames than those used here. In conclusion, taking into account SL and energy utilization (yolk and oil), temperatures close to 25°C seem to be optimal to raise snook larvae during the yolk resorption period.

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