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ABSTRACT

The effects of water temperature at 23, 27, 31, 33 and 35 °C on growth and bioenergetics of cobia *Rachycentron canadum* with initial body weights about 10, 30, 70 and 200 g were investigated in this paper. Food consumption, fecal production, nitrogenous excretion, growth rate and metabolic rate of cobia were affected significantly by both water temperature and fish size. However, the relationships between food energy and feces, excretion, growth and metabolism energy exhibited linear curves and seemed independent of water temperature and fish size in the present study. For each fish size growth increased with temperature up to 33 °C and then declined at 35 °C. The optimal temperature for growth ($T_{opt.G}$) of 10–200 g cobia was 33 °C. For each water temperature growth was negatively correlated to fish size and the model, SGR = a + blnW or SGR = aW^b, provided a good fit to the data obtained for 10–200 g cobia. Food conversion efficiency (FCE) was highest at 31 °C and lowest at 35 °C for each size cobia. The optimal temperature for FCE ($T_{opt.FCE}$) of 10–200 g cobia was 31 °C. An increasing trend of FCE with fish size was seen at each temperature and indicated that larger cobia had a superior capacity of food utilization. Energy budgets of cobia were also influenced significantly by water temperature and fish size. However, energy budgets were relatively constant over the 27-33 °C temperature and 70-200 g size ranges for cobia. Over the whole temperature and size ranges the proportion of food energy lost in feces and excretion for cobia was small (<15%) and a large proportion of food energy was allocated to growth and metabolism. The ratios of metabolism energy to assimilated energy (range: 57–84%, average: 69%) were much higher than the ratios of growth energy to assimilated energy. For cobia fast growth was attributable mainly to large food consumption though improved energy utilization with increased fish size at 27–33 °C made a certain contribution.

1. Introduction

Cobia, *Rachycentron canadum*, is a large marine finfish species distributed widely in subtropical and tropical oceans and seasonally in temperate waters (Briggs, 1960). In recent years, the potential for cobia aquaculture has been recognized because of its good meat quality, rapid growth rate and good disease resistance. In Southern China, the artificial culture of cobia has become popular and rendered aquaculture investment and development an excellent prospect. However, unlike established mari-culture fish species such as salmon, sea bass and sea bream, cobia is a recent candidate for use in aquaculture, and the knowledge on cobia is still poor though more research has been carried out in recent years (Brown-Peterson et al., 2001; Chou et al., 2001; Faulk and Joan Holt, 2005, 2006; Joan Holt et al., 2007; Liao et al., 2004; Resley et al., 2006; Rodrigues et al., 2007; Turner and Rooker, 2005; Wang et al., 2005; Webb et al., 2007; Zhou et al., 2004). In cobia aquaculture the limited information on the optimal environmental and nutritional conditions of this fish at different growth stages makes the problems of breeding failure, diet waste and water pollution more serious, which may encumber the further development of cobia aquaculture. Such problems are partly attributed to the absence of a comprehensive understanding on the bio-energetic characteristics of this fish.

The two factors—water temperature and fish size—are regarded as playing important roles in influencing growth and bioenergetics of fish (Jobling, 1994). The effects of water temperature and fish size on growth and/or bioenergetics have been reported frequently (Andersen and Riis-Vestergaard, 2003; Buckel et al., 1995; Imsland et al., 1996; Liu et al., 1998; Niimi and Beamish, 1974; Wootton et al., 1980; Xie and Sun, 1992). Some initial studies have been conducted on cobia bioenergetics (Sun et al., 2006a, 2006b, 2006c; Sun and Chen, 2009). However, little is known about growth and bioenergetics of cobia in relation to water temperature and fish size.

The present study was designed to investigate the effects of water temperature and fish size on growth and bioenergetics of cobia under laboratory conditions. Attempts were made to determine how growth and energy partition vary with water temperature and fish size, estimate the optimal temperature for growth, and furthermore improve the culture conditions of cobia.

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2. Materials and methods

2.1. Experimental fish and diet

Cobia used in the experiment were from those bred artificially by the researchers of Daya Bay Marine Biology Research Station, Chinese Academy of Sciences (MBRS).

The diet for the experimental cobia was the fresh meat of Dussumier's anchovy *Thrissa dussumieri*. Dussumier's anchovy with body weight about 50–80 g were bought from market and then handled by removing head, cauda and bones. The fish meat obtained was chopped to pieces suitable for cobia feeding. The chemical composition was 74.86% water, 16.69% protein, 4.94% lipid and 3.41% ash, and gross energy content was 5.36 kJ g^{-1} for this diet.

2.2. Fish acclimation

Fish of similar size were chosen from the outdoor breeding ponds and transferred into four indoor concrete ponds (2 × 1 × 1 m, water volume 1.6 m^3) for acclimation one week with water flow-through at 6 L min^{-1} and water temperature at 28–30 °C.

Then fish whose feeding behavior was normal were chosen and moved into the circular tanks (diameter: 80 cm, water volume: 350 L) with conical bottoms and feces-collecting bottles underneath for further acclimation. Water temperature in each tank was adjusted to the experimental temperature at a rate of 1–2 °C per day, and fish were kept at each test temperature for one more week. All experimental tanks were supplied with fresh, filtered and well-aerated sea-water of the desired temperature obtained from five different heated or cooled seawater sources (with a precision of ±0.5 °C). A flow-through system was used, and the water exchange rates were 0.5 L min^{-1}.

During the acclimation period, fish were hand-fed to satiation twice a day at about 0800 and 1700 h. Aeration was provided continuously except during feeding to maintain dissolved oxygen above 6 mg L^{-1}. Ambient photoperiod with light periods ranging from 12 to 13 h was used. Water quality variables were monitored daily.

2.3. Growth experiments

Five water temperatures (23, 27, 31, 33 and 35 °C) and four fish sizes (about 10, 30, 70 and 200 g) were tested in the growth experiment. Cobia were reared in groups of 20, 10, 5 and 2 fish per tank for 10, 30, 70 and 200 g-size classes, respectively. Four replicates were set at each temperature and size treatment. In addition, another 24 fish for 10-g-size class, 12 fish for 30-g-size class, 6 fish for 70-g-size class and 6 fish for 200-g-size class were sacrificed and used to estimate initial fish body composition and energy content, respectively.

Before starting the experiment fish were deprived of food for 36 h to empty guts. Then fish were caught individually by a nylon strainer and weighted after wiped with a moist cloth to remove excess water. A bucket with seawater was placed on an electronic balance with 0.01 g accuracy, and one by one the fish were dropped into the bucket. During the experimental period fish were hand-fed to excess twice a day (at about 0800 and 1700 h). Any uneaten food was removed from each tank 20 min after feeding, and then dried, weighed and subtracted to get the weight of food eaten by the fish. Feces were collected three to four times a day, and then weighed after drying, stored at −20 °C for subsequent chemical analysis and energy determination.

Ammonia and urea concentrations in each tank were determined using the method of Chaney and Marbach (1962). Water was sampled before and after a 24 h period of still water for the determination of ammonia and urea. During the experimental period ammonia and urea concentrations were measured three times. The energy of excretion was calculated using the conversion coefficients of 24.83 kJ g^{-1} for ammonia and 23.03 kJ g^{-1} for urea (Elliott, 1976a). Control tanks not containing fish were also set up and the values of ammonia and urea concentrations were measured to evaluate the potential loss of nitrogenous compounds through bacterial action or diffusion in experimental tanks.

Oxygen concentrations were monitored by the method of Burel et al. (1996). Changes in O_2-concentration in the inlet and outlet water of each tank were measured twice per hour at the same time as nitrogenous excretion to assess the metabolic energy demand of cobia in each water temperature and fish size group. Blank tanks without fish were used to correct O_2 variation estimated. Metabolism energy was estimated by using 13.54 kJ g^{-1} O_2 as the oxy-calorific coefficient (Elliott and Davison, 1975).

Aeration was provided continuously to maintain dissolved oxygen above 6 mg L^{-1}. Temperatures were measured twice daily and remained within ±0.5 °C of that prescribed. Salinity ranged from 31.1 to 33.7. All groups were maintained under a similar photoperiod regime of 12–13 h light.

After the 21 d experimental period for each size-class fish were starved for 36 h and then weighed individually. Fish from the same tank were killed, chopped into pieces, and then oven-dried to constant weight at 70 °C. All fish samples obtained after drying were reweighed and stored at −20 °C for analysis of body components and energy density.

2.4. Chemical analysis

All the chemical analysis methods are described in detail in Sun and Chen (2009), i.e. moisture contents were determined by oven-drying to constant weight at 70 °C, protein contents were measured by an auto Kjeldahl system (BÜCHI K-370/K-437, Switzerland), lipid contents were measured by ether extraction, ash contents were determined by a muffle furnace at 550 °C for 8–10 h, and gross energy contents were measured by an oxygenic bomb calorimeter (model 1341EE, U.S.A., calibrated by benzoic acid). Each variable was determined at least twice.

2.5. Statistical analysis

Statistical analyses were performed using SPSS 11.0 for windows ®. Differences between treatments were compared by one-way or two-way analysis of variance (ANOVA). Significance was accepted when $P < 0.05$. The relationships among food consumption, fecal production, nitrogenous excretion, growth, metabolism and fish size, were analyzed by least squares regression, and judged by coefficient of determination (R^2) and residual analysis. Data were expressed as mean ± SD of four replicates for each temperature and size treatment.

3. Results

3.1. Body chemical composition and energy content

The contents of moisture, protein, lipid, ash and energy in the body of cobia at different size and temperature treatments are listed in Table 1.

Fish chemical composition and energy content were affected significantly by both water temperature and fish size ($P < 0.05$). In a given fish size group the contents of protein, lipid and energy were higher at 27, 31 and 33 °C than at 21 and 35 °C. At each temperature the contents of protein, lipid and energy for cobia increased significantly with increasing fish size.

3.2. Food consumption

Food consumption can be expressed as grams of eaten food per fish per day (FC_a, g $fish^{-1}$ d^{-1}) or grams of eaten food per gram of fish per day (FC_r, g g^{-1} d^{-1} or % d^{-1}). For a given size FC_a increased first, peaked at 33 °C and then decreased at higher temperature, and the same trend was seen in FC_r (Table 2). At each temperature FC_a increased, but FC_r

Table 1
Body chemical composition and energy content of cobia at different temperature and size treatments.

Fish size	Temperature	Moisture content (%)	Protein content (%)	Lipid content (%)	Ash content (%)	Energy content (kJ g^{-1})
10 g	35 °C	78.13 ± 0.72 bZ	14.23 ± 0.51 abX	3.76 ± 0.20 bX	3.01 ± 0.20 aY	5.02 ± 0.21 bX
	33 °C	77.56 ± 0.43 aZ′	14.99 ± 0.40 bcX	4.24 ± 0.12 cdX	2.97 ± 0.11 aZ	5.25 ± 0.11 cX
	31 °C	77.24 ± 0.32 aZ	15.30 ± 0.28 cX	4.45 ± 0.17 dX	3.06 ± 0.14 aY	5.46 ± 0.04 dX
	27 °C	77.42 ± 0.46 aZ	15.06 ± 0.35 cX	4.16 ± 0.23 cX	2.90 ± 0.12 aZ	5.25 ± 0.17 cX
	23 °C	78.48 ± 0.39 bZ	13.88 ± 0.86 aX	3.30 ± 0.07 aX	3.41 ± 0.04 bY	4.79 ± 0.01 aX
30 g	35 °C	77.47 ± 0.48 bYZ	14.66 ± 0.18 aXY	4.03 ± 0.19 aX	2.94 ± 0.09 aXY	5.11 ± 0.12 aX
	33 °C	76.43 ± 0.41 aZ	15.32 ± 0.32 bXY	4.77 ± 0.08 bY	2.74 ± 0.27 aYZ	5.55 ± 0.15 bXY
	31 °C	76.54 ± 0.41 aY	15.41 ± 0.46 bX	4.74 ± 0.38 bXY	2.79 ± 0.16 aY	5.57 ± 0.20 bX
	27 °C	76.65 ± 0.37 abY	15.35 ± 0.26 bX	4.56 ± 0.21 bX	2.71 ± 0.21 aYZ	5.47 ± 0.02 bX
	23 °C	77.75 ± 0.62 bYZ	14.92 ± 0.61 abX	3.89 ± 0.37 aY	3.26 ± 0.08 bY	4.93 ± 0.27 aXY
70 g	35 °C	77.08 ± 0.56 bY	15.00 ± 0.50 aY	4.30 ± 0.59 aX	2.86 ± 0.12 cX	5.27 ± 0.24 abX
	33 °C	75.41 ± 0.46 aY	15.66 ± 0.50 abY	5.40 ± 0.46 bZ	2.51 ± 0.08 aXY	5.60 ± 0.15 bY
	31 °C	75.55 ± 1.01 aXY	15.72 ± 1.02 abX	5.19 ± 0.47 bY	2.68 ± 0.16 abY	5.61 ± 0.34 bXY
	27 °C	75.71 ± 0.96 aXY	16.27 ± 0.28 bY	4.97 ± 0.82 abX	2.59 ± 0.08 aXY	5.57 ± 0.37 bX
	23 °C	77.34 ± 0.58 bY	15.80 ± 0.27 abZ	4.15 ± 0.31 aY	2.78 ± 0.11 bcX	5.08 ± 0.24 aY
200 g	35 °C	74.72 ± 0.57 bX	16.47 ± 0.42 aZ	6.37 ± 0.16 bY	2.67 ± 0.15 abX	5.67 ± 0.14 abY
	33 °C	73.66 ± 0.51 aX	16.79 ± 0.19 aZ	6.96 ± 0.18 c Z′	2.43 ± 0.21 aX	5.89 ± 0.13 bZ
	31 °C	73.73 ± 0.88 aX	16.70 ± 0.74 aY	6.87 ± 0.11 cZ	2.46 ± 0.21 aY	5.90 ± 0.16 bY
	27 °C	73.85 ± 0.71 aX	16.68 ± 0.64 aY	6.75 ± 0.23 cY	2.48 ± 0.11 aX	5.86 ± 0.27 bX
	23 °C	74.82 ± 0.37 bX	16.42 ± 0.27 aZ	5.79 ± 0.36 aZ	2.86 ± 0.17 bX	5.53 ± 0.13 aZ

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abcd) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZZ′) indicate significant differences ($P < 0.05$) between fish size groups within each temperature.

decreased significantly with fish size (Table 2). The relationship between food consumption and fish size for cobia could be described by power or logarithmic function and the weight exponent b in $FC = aW^b$ ranged from 0.42 to 0.47 with a mean of 0.44 for FC_a and −0.41 to −0.37 with a mean of −0.41 for FC_r (Table 3). Two-way ANOVA showed that there was an interaction of water temperature and fish size on FC_a (temperature ∗ size: $F = 16.817$, d.f. = 19,79, $P < 0.001$) and FC_r (temperature ∗ size: $F = 7.410$, d.f. = 19,79, $P < 0.001$).

3.3. Fecal production and food absorption efficiency

In each size group, as temperature increased, fecal production of cobia showed a domed curve with a maximum at 33 °C when expressed as grams of feces per fish per day (FP_a, g $fish^{-1}$ d^{-1}), but continued to increase when expressed as grams of feces per gram of fish per day (FP_r, g g^{-1} d^{-1}) (Table 4). At a given temperature fecal production of cobia increased significantly with fish size when expressed as FP_a, whereas the contrary trend was seen in FP_r (Table 3). Two-way ANOVA showed that there was an interaction of water temperature and fish size on FP_a (temperature ∗ size: $F = 9.305$, d.f. = 19,79, $P < 0.001$).

Food absorption efficiency (FAE) of cobia at different temperature and fish size treatments is shown in Table 4. For a given size, FAE varied little with temperature though significant differences were found in some data. However, at a given temperature the variations of FAE were small though FAE slightly decreased as fish size increased.

3.4. Nitrogenous excretion

The values of nitrogenous excretion expressed as grams of N-excretion per fish per day (NE_a, g $fish^{-1}$ d^{-1}) and grams of N-excretion per gram of fish per day (NE_r, g g^{-1} d^{-1}) are listed in Table 2. In each size group NE_a increased, maximized at 33 °C, and then decreased, whereas NE_r increased continuously with temperature. At each temperature NE_a increased but NE_r decreased with fish size. The relationship between nitrogenous excretion and fish size

Table 2
Food consumption (FC) and nitrogenous excretion (NE) of cobia at different temperature and size treatments.

Fish size	Temperature	FC		NE	
		FC_a (g $fish^{-1}$ d^{-1})	FC_r (% d^{-1})	NE_a (g $fish^{-1}$ d^{-1})	NE_r (mg g^{-1} d^{-1})
10 g	35 °C	4.135 ± 0.222 bX	24.02 ± 0.91 cZ′	0.0909 ± 0.0264 bX	5.35 ± 1.89 bZ
	33 °C	6.208 ± 0.184 eX	24.87 ± 0.67 cZ′	0.1181 ± 0.0412 bX	4.67 ± 1.35 abZ′
	31 °C	5.508 ± 0.319 dX	23.43 ± 1.18 bcZ′	0.1066 ± 0.0178 bX	4.53 ± 0.71 abZ′
	27 °C	4.640 ± 0.336 cX	22.33 ± 1.40 bZ′	0.0911 ± 0.0236 bX	4.42 ± 1.30 abZ′
	23 °C	2.195 ± 0.174 aX	15.00 ± 0.09 aZ′	0.0496 ± 0.0116 aX	3.37 ± 0.61 aZ′
30 g	35 °C	8.000 ± 0.607 bY	18.37 ± 1.18 cZ	0.1654 ± 0.0259 bY	3.80 ± 0.62 cY
	33 °C	10.965 ± 0.647 dY	18.56 ± 0.43 cZ	0.2019 ± 0.0249 cY	3.41 ± 0.25 bcZ
	31 °C	9.435 ± 0.650 cY	16.96 ± 0.92 bZ	0.1827 ± 0.0126 bcY	3.29 ± 0.28 bcZ
	27 °C	8.055 ± 0.271 bY	15.77 ± 0.84 bZ	0.1584 ± 0.0331 bY	3.09 ± 0.62 bZ
	23 °C	3.835 ± 0.422 aY	9.81 ± 0.32 aZ	0.0810 ± 0.0165 aY	2.08 ± 0.40 aZ
70 g	35 °C	10.418 ± 0.775 bZ	11.79 ± 0.92 bcY	0.2299 ± 0.0222 bcZ	2.60 ± 0.24 cXY
	33 °C	14.985 ± 0.359 eZ	13.42 ± 0.89 dY	0.2777 ± 0.0531 cZ	2.48 ± 0.46 cY
	31 °C	13.745 ± 0.924 dZ	12.47 ± 0.76 cdY	0.2472 ± 0.0120 cZ	2.24 ± 0.13 bcY
	27 °C	11.198 ± 0.244 cZ	11.29 ± 0.39 bY	0.1933 ± 0.0416 bY	1.95 ± 0.44 bY
	23 °C	4.978 ± 0.420 aZ	6.36 ± 0.33 aY	0.1026 ± 0.0123 aZ	1.31 ± 0.10 aY
200 g	35 °C	16.253 ± 1.734 b Z′	7.17 ± 0.66 bcX	0.3369 ± 0.0292 cZ′	1.41 ± 0.22 cX
	33 °C	22.415 ± 1.526 d Z′	8.46 ± 0.83 dX	0.3888 ± 0.0191 dZ′	1.27 ± 0.07 bcX
	31 °C	20.213 ± 0.559 c Z′	7.98 ± 0.25 cdX	0.3494 ± 0.0114 cZ′	1.18 ± 0.02 bX
	27 °C	16.948 ± 1.800 b Z′	6.83 ± 0.37 bX	0.2949 ± 0.0276 bZ	1.09 ± 0.05 bX
	23 °C	8.390 ± 0.659 aZ′	3.82 ± 0.46 aX	0.1564 ± 0.0317 aZ′	0.69 ± 0.17 aX

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abcd) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZZ′) indicate significant differences ($P < 0.05$) between fish size groups within each water temperature.

Table 3
Coefficients of the regression equations relating food consumption (FC), nitrogenous excretion (NE) and specific growth rate (SGR) to fish size (W) of cobia.

Temperature	Item	n	Item = aW^b				Item = a + blnW			
			a	b	R^2	P	a	b	R^2	P
35 °C	FC_a	16	1.543	0.451	0.962	<0.01	−5.586	4.003	0.943	<0.01
	FC_r	16	68.71	−0.419	0.964	<0.01	37.73	−5.864	0.976	<0.01
	NE_a	16	0.033	0.447	0.883	<0.01	−0.109	0.082	0.926	<0.01
	NE_r	16	14.73	−0.423	0.854	<0.01	8.380	−1.327	0.739	<0.01
	SGR_w	16	11.85	−0.428	0.928	<0.01	6.317	−0.981	0.961	<0.01
	SGR_d	16	14.19	−0.480	0.903	<0.01	6.697	−1.075	0.946	<0.01
	SGR_p	16	13.55	−0.478	0.892	<0.01	6.506	−1.049	0.932	<0.01
	SGR_e	16	12.88	−0.407	0.884	<0.01	7.068	−1.063	0.934	<0.01
33 °C	FC_a	16	2.405	0.427	0.981	<0.01	−6.949	5.396	0.966	<0.01
	FC_r	16	62.36	−0.373	0.978	<0.01	37.80	−5.636	0.992	<0.01
	NE_a	16	0.046	0.415	0.867	<0.01	−0.103	0.092	0.911	<0.01
	NE_r	16	11.60	−0.379	0.859	<0.01	7.086	−1.069	0.758	<0.01
	SGR_w	16	14.92	−0.334	0.950	<0.01	9.676	−1.371	0.979	<0.01
	SGR_d	16	15.74	−0.335	0.931	<0.01	10.14	−1.429	0.971	<0.01
	SGR_p	16	16.40	−0.356	0.948	<0.01	10.24	−1.492	0.973	<0.01
	SGR_e	16	16.18	−0.315	0.917	<0.01	10.74	−1.465	0.963	<0.01
31 °C	FC_a	16	2.047	0.440	0.984	<0.01	−6.711	4.968	0.974	<0.01
	FC_r	16	57.60	−0.371	0.982	<0.01	35.33	−5.292	0.983	<0.01
	NE_a	16	0.044	0.401	0.959	<0.01	−0.089	0.082	0.976	<0.01
	NE_r	16	12.17	−0.406	0.956	<0.01	6.978	−1.082	0.920	<0.01
	SGR_w	16	14.07	−0.334	0.958	<0.01	9.165	−1.302	0.983	<0.01
	SGR_d	16	15.24	−0.341	0.936	<0.01	9.727	−1.387	0.977	<0.01
	SGR_p	16	16.30	−0.369	0.945	<0.01	9.925	−1.468	0.973	<0.01
	SGR_e	16	16.01	−0.324	0.919	<0.01	10.52	−1.456	0.967	<0.01
27 °C	FC_a	16	1.727	0.436	0.982	<0.01	−5.678	4.153	0.956	<0.01
	FC_r	16	59.62	−0.402	0.982	<0.01	34.25	−5.277	0.979	<0.01
	NE_a	16	0.037	0.394	0.842	<0.01	−0.073	0.067	0.858	<0.01
	NE_r	16	12.75	−0.444	0.868	<0.01	6.951	−1.121	0.771	<0.01
	SGR_w	16	12.62	−0.353	0.950	<0.01	7.889	−1.144	0.974	<0.01
	SGR_d	16	13.77	−0.362	0.929	<0.01	8.402	−1.224	0.975	<0.01
	SGR_p	16	14.50	−0.381	0.922	<0.01	8.499	−1.260	0.967	<0.01
	SGR_e	16	13.95	−0.332	0.900	<0.01	8.951	−1.246	0.957	<0.01
23 °C	FC_a	16	0.783	0.446	0.974	<0.01	−3.011	2.054	0.931	<0.01
	FC_r	16	46.84	−0.471	0.986	<0.01	23.35	−3.817	0.966	<0.01
	NE_a	16	0.020	0.386	0.859	<0.01	−0.039	0.036	0.819	<0.01
	NE_r	16	12.05	−0.531	0.924	<0.01	5.310	−0.899	0.865	<0.01
	SGR_w	16	7.968	−0.432	0.910	<0.01	4.259	−0.667	0.900	<0.01
	SGR_d	16	9.912	−0.505	0.905	<0.01	4.505	−0.740	0.883	<0.01
	SGR_p	16	8.762	−0.467	0.842	<0.01	4.291	−0.681	0.783	<0.01
	SGR_e	16	8.846	−0.422	0.851	<0.01	4.711	−0.717	0.853	<0.01
23–35 °C	FC_a	80	1.601	0.439	0.619	<0.05	−5.572	4.110	0.634	<0.05
	FC_r	80	58.70	−0.408	0.756	<0.05	33.74	−5.189	0.793	<0.05
	NE_a	80	0.035	0.408	0.594	<0.05	−0.082	0.072	0.620	<0.05
	NE_r	80	12.63	−0.437	0.745	<0.05	6.948	−1.101	0.695	<0.05
	SGR_w	80	12.06	−0.377	0.523	<0.05	7.480	−1.098	0.551	<0.05
	SGR_d	80	13.65	−0.406	0.493	<0.05	7.913	−1.176	0.534	<0.05
	SGR_p	80	13.62	−0.411	0.517	<0.05	7.912	−1.195	0.549	<0.05
	SGR_e	80	13.32	−0.361	0.480	<0.05	8.419	−1.195	0.508	<0.05

for cobia could be described by power or logarithmic function and the weight exponent b in $NE = aW^b$ ranged from 0.38 to 0.45 with a mean of 0.41 for NE_a and −0.37 to −0.54 with a mean of −0.44 for NE_r (Table 3). ANOVA showed that water temperature and fish size made significant influences on NE, and furthermore there was an interaction on NE_a (temperature ∗ size: F = 8.266, d.f. = 19,79, $P < 0.001$).

3.5. Specific growth rate and food conversion efficiency

Specific growth rate in wet weight (SGR_w), dry weight (SGR_d), protein (SGR_p) and energy (SGR_e) of cobia at each temperature and fish size treatment is listed in Table 5. Fig. 1 showed the effects of water temperature and fish size on SGR_w. In each size group SGR increased significantly with temperature up to a maximum at 33 °C followed by a significant decrease at 35 °C. However, SGR at 31 °C was only slightly lower than that at 33 °C. At 27 °C fish also grew fast though SGR was significantly lower than that at 33 and 31 °C, but higher than that at 35 °C. Fish at 23 °C showed the slowest growth rate. At each temperature a significant decline in SGR was recorded as fish size increased with a decelerating pattern. Two-way ANOVA showed that there was an interaction of water temperature and fish size on SGR_w (temperature ∗ size: F = 9.149, d.f. = 19,79, $P < 0.001$), SGR_d (temperature ∗ size: F = 6.297, d.f. = 19,79, $P < 0.001$), SGR_p (temperature ∗ size: F = 7.403, d.f. = 19,79, $P < 0.001$) and SGR_e (temperature ∗ size: F = 7.039, d.f. = 19,79, $P < 0.001$).

Food conversion efficiency in wet weight (FCE_w), dry weight (FCE_d), protein (FCE_p) and energy (FCE_e) at each temperature and fish size treatment is listed in Table 6. Fig. 1 showed the effects of water temperature and fish size on FCE_w. In each size group FCE was maximized at 31 °C though there was no significant difference between 27, 31 and 33 °C but a significant decrease was observed at 23 and 35 °C. At a given temperature FCE increased significantly with fish size though there was no significant difference between 70 and 200 g size classes. Two-way ANOVA showed that there was no interaction of water temperature and

Table 4
Fecal production (FP) and food absorption efficiency (FAE) of cobia at different temperature and size treatments.

Fish size	Temperature	FP		FAE		
		FP_a (g fish^{-1} d^{-1})	FP_r (mg g^{-1} d^{-1})	FAE_d (%) [a]	FAE_p (%) [b]	FAE_e (%) [c]
10 g	35 °C	0.0265 ± 0.0027 bX	1.54 ± 0.11 cZ′	97.44 ± 0.31 aZ	98.21 ± 0.21 abY	98.69 ± 0.13 aY
	33 °C	0.0362 ± 0.0016 cX	1.46 ± 0.15 cY	97.68 ± 0.17 abZ	98.41 ± 0.12 cY	98.81 ± 0.07 aY
	31 °C	0.0329 ± 0.0020 cX	1.40 ± 0.07 cY	97.62 ± 0.09 abZ′	98.36 ± 0.06 bcZ	98.78 ± 0.04 aZ
	27 °C	0.0252 ± 0.0029 bX	1.21 ± 0.01 bY	97.85 ± 0.13 bZ	98.53 ± 0.09 cZ	98.89 ± 0.06 sZ
	23 °C	0.0145 ± 0.0009 aX	1.00 ± 0.06 aY	97.36 ± 0.16 aZ	98.06 ± 0.11 aZ	98.64 ± 0.19 aZ
30 g	35 °C	0.0645 ± 0.0017 bcY	1.48 ± 0.04 cZ	96.78 ± 0.23 abZ	97.82 ± 0.15 bY	98.43 ± 0.12 bY
	33 °C	0.0737 ± 0.0093 cY	1.25 ± 0.23 bcY	97.31 ± 0.52 cZ	98.24 ± 0.15 cY	98.69 ± 0.21 bY
	31 °C	0.0679 ± 0.0074 bcY	1.22 ± 0.14 bY	97.13 ± 0.27 bcZ	98.17 ± 0.18 bcZ	98.61 ± 0.15 bYZ
	27 °C	0.0603 ± 0.0032 bY	1.18 ± 0.08 abY	97.02 ± 0.16 bcY	98.01 ± 0.10 bcY	98.55 ± 0.07 bY
	23 °C	0.0402 ± 0.0067 aY	1.02 ± 0.09 aY	95.85 ± 0.45 aY	97.26 ± 0.30 aY	97.97 ± 0.18 aY
70 g	35 °C	0.1192 ± 0.0076 bZ	1.35 ± 0.08 bY	95.29 ± 0.47 bY	97.20 ± 0.28 bX	97.97 ± 0.20 bX
	33 °C	0.1472 ± 0.0097 cZ	1.31 ± 0.07 bY	96.07 ± 0.31 cY	97.66 ± 0.19 cX	98.30 ± 0.14 cX
	31 °C	0.1376 ± 0.0072 cZ	1.25 ± 0.10 bY	96.03 ± 0.48 cY	97.64 ± 0.28 cX	98.29 ± 0.20 cXY
	27 °C	0.1219 ± 0.0036 bZ	1.24 ± 0.05 bY	95.70 ± 0.18 bcX	97.44 ± 0.11 bcX	98.14 ± 0.08 bcX
	23 °C	0.0735 ± 0.0056 aZ	0.96 ± 0.04 aY	94.04 ± 0.50 aXY	96.45 ± 0.30 aX	97.43 ± 0.16 aX
200 g	35 °C	0.2099 ± 0.0192 bcZ′	0.93 ± 0.13 bX	94.80 ± 0.92 abX	97.21 ± 0.46 abX	97.85 ± 0.35 abX
	33 °C	0.2441 ± 0.0250 cZ′	0.90 ± 0.10 bX	95.68 ± 0.56 cX	97.68 ± 0.09 bX	98.21 ± 0.07 bX
	31 °C	0.2360 ± 0.0165 cZ′	0.90 ± 0.07 bX	95.41 ± 0.30 cX	97.51 ± 0.13 bX	98.08 ± 0.10 bX
	27 °C	0.2021 ± 0.0169 bZ′	0.82 ± 0.10 bX	95.21 ± 0.69 cX	97.43 ± 0.37 bX	98.02 ± 0.29 bX
	23 °C	0.1354 ± 0.0133 aZ′	0.62 ± 0.09 aX	93.58 ± 0.43 aX	96.56 ± 0.23 aX	97.35 ± 0.18 aX

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abcd) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZZ′) indicate significant differences ($P < 0.05$) between fish size groups within each water temperature.

[a] FAE_d = 100 × (food intake × dry matter content − fecal production) / food intake × dry matter content.

[b] FAE_p = 100 × (food intake × protein content − fecal production × protein content) / food intake × protein content.

[c] FAE_e = 100 × (food intake × energy content − fecal production × energy content) / food intake × energy content.

fish size on FCE_w (temperature ∗ size: $F = 1.706$, d.f. = 19,79, $P > 0.05$), FCE_p (temperature ∗ size: $F = 1.210$, d.f. = 19,79, $P > 0.05$) and FCE_e (temperature ∗ size: $F = 1.005$, d.f. = 19,79, $P > 0.05$).

3.6. Energy budgets

Energy budgets among all temperature and fish size groups are shown in Table 7. In all treatments the ratios of the four terms—feces energy (F), excretion energy (U), growth energy (G) and metabolism energy (R)—in energy budgets to food energy (C) were affected significantly by water temperature and fish size ($P < 0.05$). However, only less than 15% of food energy was lost in feces and excretion and the proportion of food energy allocated to growth and metabolism was more than 80%, i.e. the value of $(F + U) / C$ was small and a very large portion of energy income was assimilated by cobia. In addition, growth energy only accounted for 18–43% of assimilated energy with a mean of 29% and most assimilated energy (A) was expended by metabolism.

In a given size group the proportions of food (or assimilated) energy retained as growth were significantly higher at 33, 31 and 27 °C than those at 21 and 35 °C, and there was no significant difference between 33, 31 and 27 °C.

At a given temperature the highest proportion of growth energy to food (or assimilated) energy was seen in the 200-g and 70-g-size

Table 5
Specific growth rate (SGR) of cobia at different temperature and size treatments.

Fish size	Temperature	IBW (g fish^{-1}) [a]	SGR_w (% d^{-1}) [b]	SGR_d (% d^{-1}) [c]	SGR_p (% d^{-1}) [d]	SGR_e (% d^{-1}) [e]
10 g	35 °C	10.34 ± 0.56 aX	4.03 ± 0.28 bZ′	4.19 ± 0.35 bZ′	4.05 ± 0.37 bZ′	4.50 ± 0.38 bZ′
	33 °C	10.30 ± 0.74 aX	6.43 ± 0.16 dZ′	6.72 ± 0.16 dZ′	6.69 ± 0.10 dZ′	7.10 ± 0.17 dZ′
	31 °C	10.21 ± 0.46 aX	6.11 ± 0.24 dZ′	6.47 ± 0.25 dZ′	6.48 ± 0.21 dZ′	6.98 ± 0.24 dZ′
	27 °C	10.47 ± 0.67 aX	5.19 ± 0.30 cZ′	5.51 ± 0.22 cZ′	5.48 ± 0.30 cZ′	5.87 ± 0.19 cZ′
	23 °C	10.61 ± 0.57 aX	2.67 ± 0.25 aZ′	2.76 ± 0.32 a Z′	2.57 ± 0.54 aZ′	2.92 ± 0.35 aZ′
30 g	35 °C	30.36 ± 0.92 aY	2.97 ± 0.29 bZ	3.02 ± 0.38 bZ	3.05 ± 0.32 bZ	3.49 ± 0.32 bZ
	33 °C	30.11 ± 1.39 aY	5.11 ± 0.31 dZ	5.36 ± 0.39 dZ	5.39 ± 0.36 dZ	6.01 ± 0.36 dZ
	31 °C	29.85 ± 1.49 aY	4.78 ± 0.24 dZ	5.02 ± 0.27 dZ	5.09 ± 0.34 dZ	5.70 ± 0.32 dZ
	27 °C	30.69 ± 1.54 aY	4.04 ± 0.24 cZ	4.25 ± 0.22 cZ	4.33 ± 0.29 cZ	4.87 ± 0.24 cZ
	23 °C	30.44 ± 1.80 aY	2.12 ± 0.27 aZ	2.10 ± 0.40 aZ	2.28 ± 0.46 aZ	2.46 ± 0.51 aZ
70 g	35 °C	68.85 ± 2.95 aZ	2.14 ± 0.29 bX	2.12 ± 0.38 bY	1.87 ± 0.39 bY	2.71 ± 0.49 bY
	33 °C	68.91 ± 1.12 aZ	3.85 ± 0.32 dY	4.17 ± 0.34 dY	3.69 ± 0.38 dY	4.71 ± 0.30 dY
	31 °C	69.83 ± 1.55 aZ	3.66 ± 0.23 dY	3.95 ± 0.25 dY	3.53 ± 0.24 dY	4.53 ± 0.31 dY
	27 °C	69.16 ± 2.38 aZ	2.98 ± 0.08 cY	3.24 ± 0.19 cY	3.10 ± 0.11 cY	3.81 ± 0.31 cY
	23 °C	68.06 ± 4.11 aZ	1.25 ± 0.23 aY	1.18 ± 0.24 aY	1.23 ± 0.16 aY	1.64 ± 0.33 aY
200 g	35 °C	199.78 ± 12.00 aZ′	1.14 ± 0.18 bX	1.03 ± 0.26 bX	1.04 ± 0.29 bX	1.34 ± 0.21 bX
	33 °C	200.26 ± 10.39 aZ′	2.39 ± 0.21 dX	2.48 ± 0.27 dX	2.39 ± 0.24 dX	2.77 ± 0.20 dX
	31 °C	196.79 ± 8.33 aZ′	2.26 ± 0.12 dX	2.33 ± 0.27 dX	2.23 ± 0.32 dX	2.65 ± 0.24 dX
	27 °C	200.21 ± 11.26 aZ′	1.84 ± 0.22 cX	1.89 ± 0.29 cX	1.81 ± 0.32 cX	2.19 ± 0.29 cX
	23 °C	202.80 ± 10.16 aZ′	0.78 ± 0.05 aX	0.65 ± 0.07 aX	0.67 ± 0.06 aX	0.86 ± 0.10 aX

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abcd) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZZ′) indicate significant differences ($P < 0.05$) between fish size groups within each water temperature.

[a] IBW = initial body weight.

[b] SGR_w = 100 × [ln(final body weight) − ln(initial body weight)] / days of the experiment.

[c] SGR_d = 100 × [ln(final body weight × final dry matter content) − ln(initial body weight × initial dry matter content)] / days of the experiment.

[d] SGR_p = 100 × [ln(final body weight × final protein content) − ln(initial body weight × initial protein content)] / days of the experiment.

[e] SGR_e = 100 × [ln(final body weight × final energy content) − ln(initial body weight × initial energy content)] / days of the experiment.

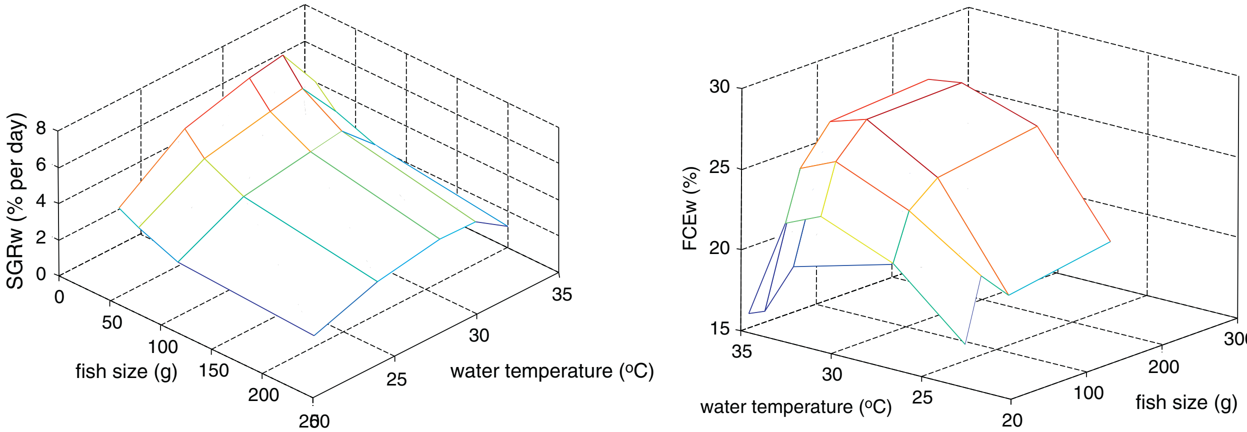

Fig. 1. Effects of water temperature and fish size on SGR_w and FCE_w of cobia.

group, and there was no significant difference between the two size classes of cobia. The lowest proportion of growth energy to food (or assimilated) energy was seen in the 10-g size group.

4. Discussion

In Dapeng Cove, Daya Bay, P.R. China, the range of water temperature is usually 17–33 °C with a mean of ~25 °C in a whole year. However, in the outside breeding ponds higher water temperature such as 35–36 °C and lower water temperature such as 13–15 °C can be recorded in summer and winter for the restricted water volume. In fact, fish growth is dependent on water temperature strongly, and too high or too low water temperature will bring negative impacts on fish growth. In this paper four water temperatures ranging from 23 to 35 °C with an interval of 4 °C were set, i.e. 23, 27, 31 and 35 °C. Furthermore, in order to describe the growth-temperature relationships of cobia in more detail, and also to determine the critical temperature at which cobia growth began to decline, referred to the previous studies by Sun et al. (2006c) and Sun and Chen (2009), another treatment of 33 °C between 31 and 35 °C was added.

Two of the most important factors affecting fish feeding are the size the fish has already reached and the temperature of water the fish inhabits. In general terms, food consumption increases first, peaks at an optimal temperature, and then decreases as temperature continues to rise (Brett and Groves, 1979). The same trend, independent of fish size, was also observed for FC over the range of 23–35 °C in this study (Table 2). The increased FC with temperature increase from 23 to 33 °C can be at least partly attributed to the increased energetic demands of fish at higher temperature for growth, activity and maintenance demands increase as ambient temperature increases not beyond the upper thermal tolerance limit for the species. However, at 35 °C the decrease in the appetite of fish was marked and from a practical point of view, there was some risk of overfeeding in cobia farming. For a certain temperature FC_a increased but FC_r decreased with increased size, i.e. larger fish consumed more food than smaller fish but had a contrary trend based on their unit weight, which indicated that food cost for unit weight of smaller fish was higher than that of larger fish.

In this paper FP of cobia were influenced significantly by water temperature and fish size. However, compared with feed type and

Table 6
Food conversion efficiency (FCE) of cobia at different temperature and size treatments.

Fish size	Temperature	FCE_w (%) [a]	FCE_d (%) [b]	FCE_p (%) [c]	FCE_e (%) [d]
10 g	35 °C	15.86 ± 1.29 aX	14.14 ± 1.21 aX	13.55 ± 1.40 aX	15.89 ± 1.36 aX
	33 °C	22.03 ± 0.49 bX	20.54 ± 0.83 bX	20.62 ± 0.53 bX	23.07 ± 0.66 bX
	31 °C	23.06 ± 1.42 bX	21.45 ± 1.27 bX	21.76 ± 1.57 bX	25.00 ± 1.40 bX
	27 °C	21.24 ± 1.95 bX	19.69 ± 1.24 bX	19.71 ± 1.26 bX	22.19 ± 1.19 bX
	23 °C	17.36 ± 1.57 aX	15.24 ± 1.88 aX	14.09 ± 3.38 aX	16.57 ± 1.40 aX
30 g	35 °C	15.68 ± 0.91 aX	14.17 ± 1.24 aX	14.01 ± 0.84 aX	16.70 ± 0.56 aXY
	33 °C	25.13 ± 1.06 cXY	24.22 ± 1.58 cXY	23.76 ± 1.47 cXY	28.38 ± 1.88 cY
	31 °C	26.07 ± 1.42 cY	25.00 ± 0.88 cXY	24.93 ± 1.22 cX	29.85 ± 1.26 cY
	27 °C	24.19 ± 1.25 cY	23.22 ± 1.65 cXY	23.26 ± 1.79 cXY	27.63 ± 1.25 cY
	23 °C	21.25 ± 2.36 bX	18.70 ± 3.40 bX	20.12 ± 4.17 bX	22.01 ± 4.79 bXY
70 g	35 °C	17.81 ± 1.53 aY	16.13 ± 2.40 aX	14.32 ± 2.64 aX	21.02 ± 3.56 aZ
	33 °C	27.40 ± 3.52 bY	28.20 ± 3.81 bYZ	24.54 ± 3.99 bYZ	32.38 ± 3.84 bYZ
	31 °C	28.06 ± 1.99 bY	28.75 ± 3.36 bXY	25.37 ± 2.84 bXY	33.68 ± 3.98 bYZ
	27 °C	25.59 ± 1.33 bY	26.24 ± 2.50 bYZ	25.65 ± 1.66 bY	31.54 ± 4.37 bYZ
	23 °C	19.43 ± 2.73 aX	16.64 ± 2.60 aX	18.15 ± 1.35 aX	23.35 ± 4.21 aY
200 g	35 °C	15.78 ± 1.21 aX	14.38 ± 2.30 aX	14.31 ± 2.88 aX	19.24 ± 1.85 aYZ
	33 °C	27.78 ± 1.80 cY	29.92 ± 3.23 bZ	27.92 ± 2.44 bZ	34.24 ± 3.57 bZ
	31 °C	28.17 ± 1.98 cY	29.75 ± 3.66 bZ	27.90 ± 4.90 bY	35.04 ± 4.00 bZ
	27 °C	26.61 ± 2.56 cY	28.22 ± 3.54 bZ	26.15 ± 4.22 bY	33.45 ± 3.85 bZ
	23 °C	20.54 ± 1.65 bX	17.41 ± 2.70 aX	17.74 ± 3.53 aX	23.18 ± 4.41 aY

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abc) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZ) indicate significant differences ($P < 0.05$) between fish size groups within each water temperature.

[a] FCE_w = 100 × (final body weight − initial body weight) / food intake.
[b] FCE_d = 100 × [(final body weight × final dry matter content) − (initial body weight × initial dry matter content)] / (food intake × dry matter content).
[c] FCE_p = 100 × [(final body weight × final protein content) − (initial body weight × initial protein content)] / (food intake × protein content).
[d] FCE_e = 100 × [(final body weight × final energy content) − (initial body weight × initial energy content)] / (food intake × energy content).

Table 7
Energy budgets[a] of cobia at different temperature and size treatments.

Fish size	Temperature	C (kJ g^{-1} d^{-1})	% C				% (C-F-U)	
			F	U	G	R	G	R
10 g	35 °C	1.287 ± 0.049 cZ′	1.31 ± 0.16 bcX	10.27 ± 3.41 aX	15.89 ± 1.36 aX	73.63 ± 5.97 bX	18.00 ± 1.70 aX	83.20 ± 4.49 bX
	33 °C	1.333 ± 0.036 cZ′	1.19 ± 0.09 abX	8.75 ± 2.80 aX	23.07 ± 0.66 bX	65.14 ± 7.52 aY	25.64 ± 1.37 bcX	72.45 ± 9.29 aY
	31 °C	1.255 ± 0.063 bcZ′	1.22 ± 0.04 bX	8.96 ± 1.43 aX	25.00 ± 1.40 bX	64.29 ± 3.39 aY	27.83 ± 1.64 cX	71.62 ± 4.62 aZ
	27 °C	1.197 ± 0.075 bZ′	1.11 ± 0.06 aX	9.15 ± 2.51 aX	22.19 ± 1.19 bX	66.15 ± 4.58 aY	24.75 ± 1.64 bX	73.72 ± 4.93 aY
	23 °C	0.804 ± 0.005 aZ′	1.36 ± 0.08 cX	10.40 ± 1.84 aX	16.57 ± 1.40 aX	70.83 ± 3.91 abY	18.78 ± 1.61 aX	80.31 ± 5.05 abX
30 g	35 °C	0.985 ± 0.063 cZ	1.57 ± 0.11 bcX	9.69 ± 2.30 aX	16.70 ± 0.56 aXY	69.12 ± 5.99 bX	18.81 ± 0.32 aXY	77.91 ± 6.76 bX
	33 °C	0.995 ± 0.023 cZ	1.31 ± 0.26 aX	8.50 ± 0.55 aX	28.38 ± 1.88 cY	59.71 ± 3.96 aX	31.47 ± 2.21 cY	66.20 ± 4.30 aXY
	31 °C	0.909 ± 0.049 bZ	1.40 ± 0.13 abY	9.01 ± 1.06 aX	29.85 ± 1.26 cY	57.52 ± 1.77 aX	33.30 ± 1.34 cY	64.14 ± 2.24 aY
	27 °C	0.845 ± 0.045 bZ	1.45 ± 0.08 abY	9.11 ± 1.90 aX	27.63 ± 1.25 cY	59.14 ± 7.71 aXY	30.90 ± 1.46 cY	66.14 ± 8.75 aXY
	23 °C	0.526 ± 0.017 aZ	2.02 ± 0.22 cY	9.78 ± 1.69 aX	22.01 ± 4.79 bXY	67.33 ± 4.76 bX	24.93 ± 5.37 bXY	76.33 ± 5.10 bX
70 g	35 °C	0.632 ± 0.049 bcY	2.03 ± 0.20 bY	9.69 ± 2.30 aX	21.02 ± 3.56 aZ	66.17 ± 6.39 bX	23.92 ± 3.76 aZ	75.44 ± 7.14 cX
	33 °C	0.719 ± 0.043 dY	1.70 ± 0.14 aY	8.50 ± 0.55 aX	32.38 ± 3.84 bYZ	52.04 ± 4.56 aX	41.57 ± 1.47 cZ	58.05 ± 5.59 aX
	31 °C	0.668 ± 0.041 cdY	1.71 ± 0.20 aY	9.01 ± 1.06 aX	33.68 ± 3.98 bYZ	51.82 ± 1.69 aX	42.88 ± 3.04 cZ	57.61 ± 1.97 aX
	27 °C	0.605 ± 0.021 bY	1.86 ± 0.08 abZ	9.11 ± 1.90 aX	31.54 ± 4.37 bYZ	55.40 ± 2.97 abX	34.98 ± 4.85 bYZ	61.46 ± 3.68 abX
	23 °C	0.341 ± 0.018 aY	2.57 ± 0.22 cZ	9.78 ± 1.69 aX	23.35 ± 4.21 aY	63.69 ± 14.61 bX	26.53 ± 4.50 aY	72.47 ± 16.61 bcX
200 g	35 °C	0.384 ± 0.035 bcX	2.15 ± 0.35 abZ	9.71 ± 1.68 bX	19.24 ± 1.85 aYZ	67.43 ± 2.96 bX	21.83 ± 2.19 aYZ	76.50 ± 2.87 bX
	33 °C	0.454 ± 0.045 dX	1.79 ± 0.07 aZ	8.07 ± 0.87 aX	34.24 ± 3.57 bZ	53.35 ± 3.21 aX	37.99 ± 4.07 bZ	59.17 ± 3.40 aX
	31 °C	0.423 ± 0.015 cdX	1.92 ± 0.10 abZ	8.00 ± 0.31 aX	35.04 ± 4.00 bZ	52.49 ± 4.12 aX	38.90 ± 4.41 bZ	58.27 ± 4.55 aXY
	27 °C	0.366 ± 0.020 bX	1.98 ± 0.29 abZ	8.06 ± 0.42 aX	33.45 ± 3.85 bZ	56.79 ± 1.97 aX	37.17 ± 4.16 bZ	63.13 ± 2.49 aX
	23 °C	0.205 ± 0.025 aX	2.65 ± 0.18 bZ	8.62 ± 1.47 abX	23.18 ± 4.41 aY	64.86 ± 3.20 bX	26.16 ± 5.12 aY	73.10 ± 3.27 bX

Letters after each value indicate results of pair-wise comparisons. Different lower case letters (abcd) indicate significant differences ($P < 0.05$) between water temperatures within each fish size group; different upper case letters (XYZZ′) indicate significant differences ($P < 0.05$) between fish size groups within each water temperature.
[a] C = F + U + R + G (Brett and Groves, 1979), where C is energy intake, F is energy lost in feces, U is energy lost in excretion, R is energy consumed by metabolism and G is energy stored as growth.

composition, water temperature and fish size are not the particular important factors affecting FP (Jobling, 1994). Fig. 2 showed that increased FC led to increased FP regardless of water temperature and fish size used in the experiment after conversion to the energy values. Food absorption efficiency has been reported to be influenced by factors such as feed type, ration level, water temperature, fish size and feeding regime, but under most circumstances the effects of ration level, water temperature and fish size will rarely be of major proportions for the variation of FAE is relatively small (Jobling, 1994). In this study, apparent FAE was relatively stable though there were significant differences of FAE in some data. It could be speculated that there might be some adaptative mechanisms to regulate the capability of fish to digest food correctly over a certain range of water temperature and fish size.

Water temperature and fish size are two important factors having great influence on endogenous nitrogen excretion, and ingestion of food will lead to an increase in exdogenous nitrogen excretion (Jobling, 1994). In the paper NE of cobia was affected significantly by water temperature and fish size. However, the variations of NE among different temperature groups were not as much as those among different size groups for cobia. Actually, in some studies (Kaushik, 1981; Kikuchi et al., 1995), compared with factors such as food intake and fish size, direct effects of water temperature on NE were minor. Savitz (1969) reported that, NE of bluegill sunfish *Lepomis macrochirus* appeared to change little between 7 and 15.6 °C. Similar findings of smaller influence of water temperature on NE in comparison with fish size were observed for cobia in the tested temperature and size ranges.

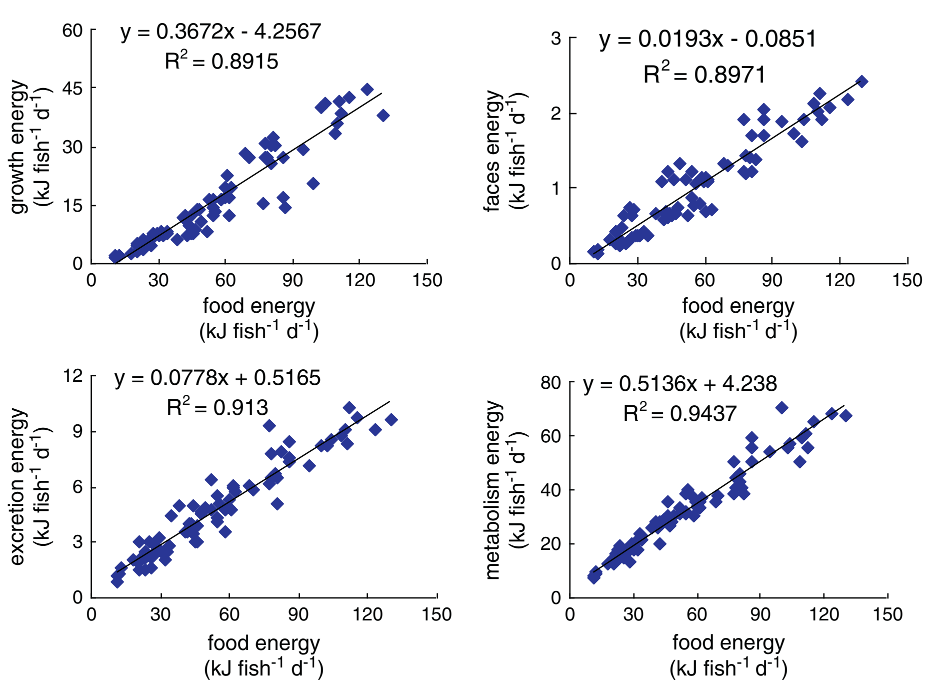

Fig. 2. Relationships between growth, feces, excretion, metabolism energy and food energy.

Likewise, linear relationship between NE and FC of cobia was also seen in Fig. 2 after conversion to the energy values and seemed independent of water temperature and fish size, which indicated that changes of NE resulted mainly from FC though direct effects of water temperature and fish size used in the experiment existed.

In the present study growth rates of cobia were significantly affected by water temperature and fish size as well as their interaction. In general, as temperature increases growth increases first, peaks at an optimal temperature, and then declines at higher temperatures. However, considering the different temperature ranges studied in literatures the pattern used to describe the SGR–T relationship took various forms: $SGR = a + bT + cT^2$ (Burel et al., 1996; Imsland et al., 1996) or $SGR = a + bT + cT^2 + dT^3$ (Person-Le Ruyet et al., 2004) for a domed curve, $SGR = a + b\ln T$ (Liu et al., 1998; Russell et al., 1996) or $SGR = aT^b$ (Wurtsbaugh and Cech, 1983) for a decelerating curve, and $SGR = a + bT$ for a linear curve (Allen and Wootton, 1982), etc. In this paper the optimum growth temperature ($T_{opt.G}$) was estimated to be 33 °C though 31 °C was also very suitable for fish growth. However, according to the theory as presented by Imsland et al. (1996) and Jonassen et al. (1999), $T_{opt.G}$ is usually higher than the temperature the species meet in nature. In fact, the ambient temperatures for cobia marine-cage culture in Southern China seldom rise up to 33 °C. A significant decrease in SGR was found between 33 and 35 °C, which indicated that this was the upper temperature limit for cobia growth in seawater. Over the temperature range of 23–35 °C, no model is so well fitted to the experimental data obtained for cobia in this study though a quadratic function was ever used to describe the SGR–T relationship of juvenile cobia roughly (Sun et al., 2006c, Sun and Chen, 2009), for the curves were asymmetrical with a rapid decline in growth rate above $T_{opt.G}$.

No change in $T_{opt.G}$ was observed in this paper, i.e. $T_{opt.G}$ was size-independent for cobia over the size range of 10–200 g, which was in accordance with the studies on mandarin fish *Siniperca chuatsi* (Liu et al., 1998), brown trout *Salmo trutta* L. (Elliott, 1975) and sockeye salmon *Oncorhynchus nerka* (Brett, 1979). However, for some other species such as Atlantic cod *Gadus morhua* (Pedersen and Jobling, 1989), Chinese snakehead *Channa argus* (Liu et al., 1998), plaice *Pleuronectes platessa* (Fonds et al., 1992), turbot *Scophthalmus maximus* L. (Imsland et al., 1996) and Atlantic halibut *Hippoglossus hippoglossus* L. (Björnsson and Tryggvadóttir, 1996) $T_{opt.G}$ tended to decrease with increased fish size. Interspecific difference or a narrow fish size range in experiments may, in part, explain this discrepancy. So more studies are needed on the growth–temperature relationships of different fish species over a wider fish size range to answer this question.

As a rule fish growth rate decreases with increased fish size and the relationship between growth and fish size takes a decelerating-curve form described as $SGR = aW^b$ or $SGR = a + b\ln W$ (Jobling, 1994). Based on a review of published results the exponent b in $SGR = aW^b$ could range from −1.0 to 0.7 and was often −0.40 for fish fed satiation (Jobling, 1983). In this paper the relationships between growth rate and fish size at different water temperatures could be described as power and logarithmic functions (Table 4). The b values in $SGR = aW^b$ of cobia ranged from −0.315 to −0.505 with a mean of −0.377, and somewhat different as temperature changed though the variation was not large. In the study on rainbow trout *Salmo gairdnerii* R. (Wangila and Dick, 1988) the b value was −0.41–−0.24 at 15 °C, but ranged from −0.74 to −0.01 at 7 °C, and in the study on Chinese snakehead *C. argus* (Liu et al., 1998) the b value changed with temperature and tended to decrease with increasing temperature, i.e. for some fish species the exponent b in $SGR = aW^b$ was temperature-dependent. In the studies on Atlantic halibut *H. hippoglossus* L. (Björnsson, 1995; Björnsson and Tryggvadóttir, 1996) the b value was −0.46 for fish weighing 10 g–5 kg but was about −1.0 for fish weighing 2–12 kg, and in the studies on brook trout *Salvelinus fontinalis* (Cooper, 1961; Haskell, 1959) the b value was −0.33 for fish weighing 1.5–60 g but was −0.47 for fish weighing 2.5–350 g, i.e. for some fish species the exponent b in $SGR = aW^b$ was also size-dependent. Based on the wide range of the b value reported in many papers and the fact that the exponent b in $SGR = aW^b$ was not always a fixed value and might be affected by the factors such as fish species, water temperature and fish size, it is necessary for cobia to perform further studies on the SGR–W relationship.

FCE is also influenced by water temperature and fish size, especially water temperature. In the present study for a given size FCE of cobia was highest at 31 °C and lowest at 35 °C, but minor changes were observed over the temperature range of 27–33 °C, which agreed with the previous findings reported by Sun et al. (2006c) and Sun and Chen (2009), i.e. the capacity of food utilization for cobia was superior at 27–33 °C and somewhat depressed outside this thermal range. The optimum temperature for FCE ($T_{opt.FCE}$), usually defined as the temperature giving maximum FCE, was estimated to be 31 °C though high FCE was also obtained at 27 and 33 °C for four size classes of cobia. Data showed that $T_{opt.FCE}$, independent of fish size, was slightly below $T_{opt.G}$ for 10–200 g cobia, which agreed with the studies on Atlantic salmon *Salmo salar* (Handeland et al., 2008), Atlantic cod *G. morhua* (Björnsson et al., 2001) and turbot *S. maximus* L. (Imsland et al., 2001). The supposed explanation for this finding is that growth rate reaches a maximum at a temperature equal to or lower than the temperature giving maximum ingestion rate at unrestricted ration and growth rate increases more than ingestion rate before temperature rises up to $T_{opt.G}$. At a fixed temperature FCE of 200-g-size fish did not differ significantly from that of 70-g-size fish, but was significantly higher than that of 10-g-size fish, which indicated that the capacity of larger cobia to utilize food was superior to the smaller.

The energies of growth, feces, excretion and metabolism all increased linearly with food energy over the experimental temperature and size ranges for cobia (Fig. 2). Water temperatures in the natural habitats of cobia range from 10 to 35 °C though in most cases fish are found in the sea area of 25–32 °C and seldom appear at the upper and lower temperature limits. In the present study the experimental temperatures (23–35 °C) were among the range suitable for cobia living though high temperature at 35 °C and low temperature at 23 °C had depressed impacts on fish growth during the 21 d experimental period. The consequence for the positive linear relationships between growth, feces, excretion, metabolism energy and food energy is that (1) growth, fecal production, nitrogenous excretion and metabolism are tightly linked with food consumption, (2) the effect of various FCE at different temperature and size treatments on growth can be neglected to some extent, and (3) the more food consumption, the more growth retain, feces and N-excretion waste and metabolism exhaustion over the temperature range of 23–35 °C.

For a given size the ratios of growth energy to food (or assimilated) energy (G/C or G/A) were much higher at 27, 31 and 33 °C than at 23 and 35 °C, i.e. over the experimental temperature range, G/C (or G/A) were temperature-dependent and the living regions with ambient temperature of 27–33 °C were more beneficial to the energy utilization of cobia. At a given temperature G/C (or G/A) of 70-g and 200-g-size fish were significantly higher than that of 30-g and 10-g-size fish, i.e. over the experimental size range G/C (or G/A) were size-dependent and larger cobia were more efficient in converting food energy into growth energy than smaller fish. However, G/C were size-independent for southern catfish *Silurus meridionalis* Chen weighing from 8.69 g to 127.4 g at 25 °C (Xie and Sun, 1992). So the question can now be posed of whether the phenomenon observed in cobia, the utilizing efficiency of food energy is improved somewhat with increased fish size over a certain size range, can occur in a wider range of fish species.

Over the water temperature and fish size ranges investigated in the study the allocations of food (or assimilated) energy to growth (Average: 26% for G/C and 29% for G/A) were much less than to metabolism (Average: 62% for G/C and 69% for G/A) irrespective of water temperature and fish size. Cobia is a carnivorous, coastal pelagic fish with characteristics of migrating long distance and hunting ferociously, which might result in a large energy demand for metabolism. However, the other features for cobia are their rapid growth and large size though energy expended in prey-hunting, cruising, and food digestion constitutes a major proportion of food energy. According to the data of FC, SGR, FCE and energy budgets, it could be speculated that fast growth resulted mainly from large food consumption though improved energy utilization with increased fish size at 27–33 °C made a certain contribution for cobia.

Cui and Wootton (1988) observed that the energy allocation pattern in minnows *Phoxinus phoxinus* (L.) (1–5.4 g) fed maximum rations was independent of temperature over the experimental temperature range of 5–15 °C. Pandian (1982) reported that energy budgets of *Channa striatus* (Bloch 1797) were relatively constant between 22 and 37 °C though the ratio of growth energy to food energy at 17 °C was far too low over the experimental temperature range of 17–37 °C. The proportions of food energy allocated to each component of energy budget of brown trout *S. trutta* L. did not vary much over the 5–13 °C temperature range and the 11–260 g size range based on the data by Elliott (1976b). In this paper cobia exhibited the similar phenomenon of constant energy allocation between 27 to 33 °C and 70 to 200 g though energy budgets differed significantly over the whole experimental temperature and size ranges of 23–35 °C and 10–200 g.

In conclusion, the results from the present study provide important information for commercial rearing of cobia. However, the factors such as experimental methods, feed type and composition, ration level, fish density, photoperiod, salinity, DO, and pH are also known to influence fish growth and bioenergetics. Moreover, in the laboratory experiment only a batch of fish was used and the fish were held at low density in laboratory conditions, which made it uncertain whether the results can be generalized to the context of aquaculture.

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