EFFECTS OF PARTIAL AND COMPLETE FOOD DEPRIVATION ON COMPENSATORY GROWTH OF JUVENILE SOFT-SHELLED TURTLE (*PELODISCUS SINENSIS*): TEMPORAL PATTERNS IN GROWTH RATE AND CHANGES IN BODY COMPOSITION

XIE Zhi-Gang and NIU Cui-Juan

(*Ministry of Education Key Laboratory of Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875*)

Abstract: To ascertain compensatory growth capability of juvenile soft-shelled turtles (*Pelodiscus sinensis*), the turtles with an average body weight of 9.56g were treated with one of the following regimes: full food deprivation for 0 (control), 1, 2, 3 and 4 weeks, respectively; Partial deprivation by feeding with the equivalent of one per cent of mean body weight for 4 weeks, and then the turtles in each group were fed to apparent satiation until the end of the 10-week experiment. Each fully food deprived group showed significantly higher specific growth rate than the control during the first re-feeding week, but the final body weight of all food deprived groups did not exceed the control. By the end of the deprivation period, body lipid content showed a decreasing trend with increasing duration of food deprivation, while body ash and moisture contents showed a clear reverse trend: lipid content was significantly lower in each deprived group than the control, but ash content or moisture content was significantly higher than the control. No significant differences were found in protein content among all groups. Final body lipid, protein and moisture restored to the control level, but ash did not. The results indicated that the juvenile turtles subjected to starvation firstly consumed fat as their main energy source, and full food deprivation could trigger a partially compensatory growth response, whereas partial deprivation failed to introduce the compensatory response.

Key words: Soft-shelled turtle; *Pelodiscus sinensis*; Compensatory growth; Starvation; Body composition

CLC number: S966.5 **Document code:** A **Article ID:** 1000-3207(2007)02-0214-06

In animal kingdom, some species are able to modify their growth rates in response to fluctuations in food availability. Compensatory growth is an interesting physiological response of the animals subjected to starvation. It has not only ecophysiological significance, but potential importance to farm industry and resource management. If the starved animals display a rapid growth spurt when switched to a food-abundant condition and consequently catch up or exceed the body weight of those being fed enough consistently, the compensatory response is named as completely compensatory growth or over-compensatory growth[1,2], respectively; If finally the starved animals can not catch up with those being fed enough consistently in body weight in spite of ever possessing higher growth rate, the compensatory response is named as partially compensatory growth[3].

Compensatory growth has been intensively studied in a variety of animal taxa, such as domestic animals, fishes, mollusks and crustaceans, and the results are diverse[2,4—6]. However, few studies are available on compensatory growth of aquatic turtles under experimental condition. Soft-shelled turtle (*Pelodiscus sinensis*) is an important aquaculture species in China. We have reported some studies on its bioenergetics and nutritional require-

Received date: 2005-10-11; **Accepted date:** 2006-11-26

Foundation item: the National Natural Science Foundation of P. R. China (project No. 30271014)

Brief introduction of the author: XIE Zhi-Gang (1978—), male, born in Zhangjiakou, Hebei Province; doctor; engaged in molecular and physiological ecology

Corresponding author: Niu Cui-Juan, Prof; E-mail: cjniu@bnu.edu.cn

ments[7—9], but little is known about compensatory growth of this species. Purpose of the present study was to obtain knowledge of compensatory growth capacity of juvenile soft-shelled turtles under different feeding regimes.

1 Materials and Methods

The experimental turtles were obtained from a hatchery in Shijiazhuang, China, and acclimated to laboratory conditions of a fixed photoperiod of 12L: 12D at the temperature of maximal growth (30℃)[8] for two weeks. During this period, all the animals were fed to apparent satiation twice a day on a commercial formulated feed powder (mean composition as percentage of dry matter: crude protein 44%, crude lipid 6% and ash 16%), which was blended with water and extruded to soft pellets before use.

Prior to the trial, all turtles were starved for 24 h to empty the gut. Each animal was then toweled off and weighed to 0.01g with an electronic balance. Three animals were sampled randomly for initial body composition analysis. The animals sampled were anaesthetized by ether and then froze to death at the temperature of −20℃. Seventy two turtles with a mean body weight of 9.56±1.57g were chosen, and randomly divided into six groups. Each group was placed in one glass aquarium with the dimension of 90cm × 60cm × 50cm, which was enough for the 12 turtles to avoid space competition and fighting. A code was marked with water-insoluble lacquer on each animal's shell to differentiate it from the others. Six treatment regimes are as follows: starved for 0 (control), 1 (S1), 2 (S2), 3 (S3) and 4 (S4) weeks respectively or fed with the equivalent of one percent of mean body weight for 4 weeks (R). Then, all turtles were fed to apparent satiation (about 6% of mean body weight) by the end of the 10-week experiment. When food deprivation or restriction regime was terminated in a group, three animals were sampled randomly for body composition analysis, and then adequate food was supplied to the remainder individuals in the group twice daily. Food was placed in different positions of the aquarium to guarantee satiation of each animal, and the remnant was removed after 30 min for preserving water quality. Once a week, all of the turtles were weighed, aquaria were cleaned and on that day the animals were not fed. At the end of the trial, all the experimental animals were weighed after being food deprived for 24 h, and three turtles were sampled at random in each group for body composition analysis.

All turtles sampled were dried at 65℃ to a constant weight for determination of water content, and then homogenized by a minitype muller for body composition determination. We determined protein content by Kjelldahl analysis and protein content was calculated from nitrogen by multiplying by 6.25. Lipid content was determined by the chloroform-methanol extraction. Ash content was determined by combustion at 550℃ for 12 h.

Specific growth rate (SGR) in body weight was computed as follows: SGR (%/day) = $100(\mathrm{Ln}\ W_t - \mathrm{Ln}\ W_i)/T$, where W_t and W_i are final and initial weight in grams respectively during each growth period, T is duration of growth period (d).

As there were marked differences in body weight at the start of refeeding among different treatments, analysis of covariance (ANCOVA) with body weight at the beginning of refeeding as covariate, was utilized to compare SGR among the treatments. In the process, SGR was corrected for the effect of body weight, and Least-significant difference (LSD) test was employed to assess the effects of treatments. One-way analysis of variance (ANOVA) tested the differences in initial body weight, final body weight and body composition. The Tukey HSD test was carried out for making pair-wise comparisons between means in different groups, and $p < 0.05$ was taken as the level of significance. All statistical analyses were performed using the SPSS10.0 software package.

2 Results

No animal died during the experiment, but two animals in S4 showed bad health at the end of starvation and anorexia during the refeeding period.

Changes in body weight among treatments are presented in Tab. 1. At the start of refeeding, significant differences were found between the deprived groups and the control, and also among the deprived groups ($F_{5,68}$ = 18.85, $p < 0.001$). Body weight declined with the duration of full food deprivation. Body weight in the food restricted group (R) was significantly higher than that in each fully food deprived group, while significantly lower than that in the control. At the end of the experiment, body weight still varied among the deprived groups ($F_{5,48} = 27.56, p < 0.001$), and all were less than mean body weight of the control group.

Tab. 1 Changes in body weight (Mean±SEM) of experimental groups during the experiment; letters after each value indicate results of Tukey HSD test. Values not sharing a common letter are significantly different at the 0.05 level

Group	Initial body weight (g)	Body weight after full or partial deprivation (g)	Final body weight (g)
	N= 12	N= 12	N= 9
S1	9.92±0.25	8.75±0.29[c]	36.50±1.78[b]
S2	9.94±0.39	8.32±0.44[c]	31.54±1.85[bc]
S3	9.58±0.29	7.10±0.36[cd]	29.56±0.86[cd]
S4	9.98±0.30	6.67±0.37[d]	22.14±1.43[d]
R	9.32±0.38	11.99±0.76[b]	34.22±1.85[bc]
Control	9.71±0.46	19.59±1.0[a] (week 4)	45.98±2.51[a]

During the period of food deprivation, the fully food deprived turtles had negative specific growth rates (SGR) (Fig. 1), and the food-restricted animals had a lower SGR than the control (Fig. 1). During the refeeding weeks, the results of the repeated ANCOVA showed that SGR of the fully food deprived turtles increased significantly relative to the control (Fig. 2) ($F_{4,42} = 6.735$, $p < 0.001$) in the first refeeding week, and subsequently declined to the level of the control group in the following refeeding week. The SGR in S4 remained significantly higher than that in S1 or S2 during the third refeeding week ($F_{4,42} = 4.064, p < 0.05$).

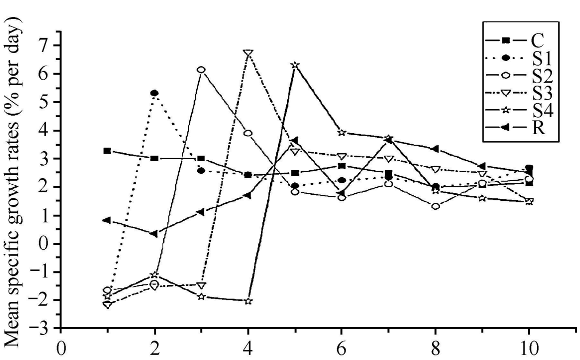

Fig. 1 Temporal patterns of changes of mean specific growth rates (% per day) of the soft-shelled turtles during the experiment: fully food-deprived groups S1-S4, food-restricted group (R) and the control group

No significant increase was measured in SGR between group R and the control during 1-3 refeeding weeks. However, SGR in R was significantly higher than that in S4 during the fourth refeeding week (Fig. 2) ($F_{2,26} = 6.685$, $p < 0.05$).

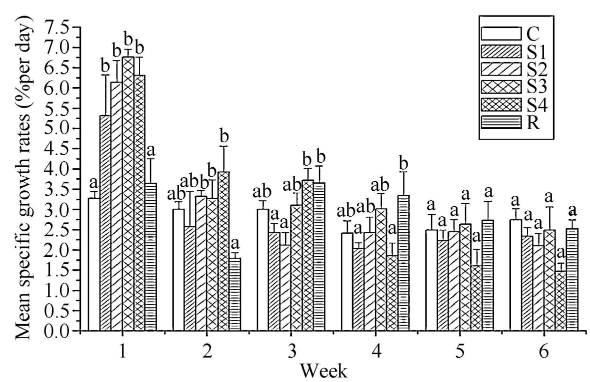

Fig. 2 Comparisons of mean specific growth rates (mean±SEM, % per day) of the soft-shelled turtles among the groups during the anterior six weeks of the refeeding period of each group: fully food-deprived groups S1-S4, the food restricted group (R) and the control group (The 1-6 week SGRs of the control group were used as the controls which were compared with the SGRs of other groups, respectively). Values not sharing a common letter are significantly different ($p < 0.05$)

The result of body composition changes is shown in Tab. 2. After full or partial deprivation, protein contents were not significantly different between the deprived groups and the control, as well as among the deprived groups ($F_{5,12} = 0.264, p > 0.05$), while lipid (or fat) contents in all the deprived groups declined significantly relative to the control ($F_{5,12} = 39.075$, $p < 0.001$). Furthermore, the lipid contents showed a diminishing trend with increasing duration of deprivation. There were significant increases in both moisture and ash contents in the fully deprived groups compared with the control ($F_{5,12} = 29.122$, $p < 0.001$; $F_{5,12} = 9.323$, $p = 0.001$), and both contents showed an increasing trend with the increasing duration of full deprivation. At the end of the trial, all the body compositional contents, except ash content ($F_{5,12}$= 34.571, $p < 0.001$), restored to the control level. The final ash content in S4 was still the highest.

Tab. 2 Body biochemical composition of the soft-shelled turtles at different stages of the experiment; values are means± SEM of concentration of protein, lipid, ash (expressed as % dry weight, % DW) **and moisture** (expressed as % fresh weight, % FW); **significant differences within the same column are denoted by different letters** ($p < 0.05$)

	Protein (% DW)	Lipid (% DW)	Ash (% DW)	Moisture (% FW)
Initial	60.22±4.37	16.94±2.60	17.32±1.07	78.59±3.41
After full or partial deprivation				
C	61.65±2.14	20.47±0.76[c]	13.98±0.81[a]	73.12±1.29[a]
S1	62.05±2.87	14.87±5.49[b]	16.88±0.57[b]	76.72±2.19[b]
S2	61.34±1.04	14.40±1.19[b]	17.95±0.46[b]	78.56±2.30[b]
S3	61.29±1.58	9.27±0.31[a]	21.78±1.31[c]	80.74±3.23[c]
S4	59.34±2.17	6.90±0.70[a]	23.47±1.09[c]	83.03±1.89[c]
R	62.03±6.91	12.87±1.33[b]	16.72±1.54[b]	77.75±3.45[b]
Final				
C	61.97±1.48	18.07±1.60	13.71±0.95[a]	73.62±3.51
S1	61.64±3.42	17.37±1.70	15.26±1.32[b]	73.84±2.35
S2	61.37±1.50	18.30±1.21	15.81±0.65[b]	74.56±1.94
S3	60.91±2.71	17.27±0.15	16.04±0.79[b]	73.55±3.17
S4	58.22±4.58	16.90±1.30	19.07±0.53[c]	73.53±2.52
R	61.88±3.44	18.10±1.93	14.67±1.42[b]	74.12±1.633

3 Discussion

Compensatory growth is considered as an adaptation to a lifestyle with widely fluctuation of food resources. Under natural conditions, soft-shelled turtles experience alternating periods of feast and famine. Thus, they maybe need strive to lessen variation in body weight for competition and survival. In our study, the severity of food deprivation was responsible for the different growth responses adopted by the turtle. The fully deprived groups showed accelerated growth when restored to satiation, although final body weight did not exceed the control, which revealed a partially compensatory growth pattern in the fully food deprived turtles but not in the partially food deprived ones. Similar compensatory growth patterns were reported in some fish species, such as *Arctic charr*[3,10] hybrid tilapia (*Oreochromis mossambicus Peters* × *O. niloticus L.*)[11] and fry of cyprinid species[12]. However, the definition of severity of food deprivation should include two aspects: the abundance of available food and the duration of starvation. In terms of the later, completely compensatory growth happened within a shorter duration of food deprivation in the above fish species. Therefore, it seems that there might be a point of no return or a threshold in the duration of starvation, i.e. animals will not recover their body weight fully if the time of starvation overruns this threshold. More detailed studies on whether the threshold exists in the turtle will be carried out in the future.

Unequal food acquisition can result in increased variability in growth because of competition for the limited resource[13—17], and leads to marked difference in individual body weight, which is possibly harmful to aquaculture. In the present study, the turtles under the food restricted regime obviously showed more variances in individual weight than those under the control and the fully deprived regimes (Tab. 1). Starvation or malnutrition can always deflect animal's physiological age from its chronological age, usually represented as differences in body sizes and growth rates. As for experimental design, it is suggested that comparisons of compensatory growth rates should be based on physiological age[18] or similar body weight[11]. So we used body weight at the beginning of refeeding as covariate by ANCOVA to compare SGR among the treatment groups.

During the food-deficient period, most animals firstly mobilize stored fat, rather than stored protein as their main energy resource, and restore fat reserves when switched to a food-abundant condition. However, Maddock & Burton[18] found that the winter flounder (*Pleuronectes americanus*) mainly depletes protein during the starvation period. In the current study, fat content of the turtle was diminished with the increasing duration of starvation, and then restored to the control level after refeeding, which agrees with most of the results published in other species[11, 19].

The mechanism of compensatory growth is inconclusive and varies in different species. Usually, starved animals recover their weight loss by increasing food consumption as in some fish species[3, 11, 15], or by improving food conversion as in European minnows[4]. In the current work, although we could not quantify feed intake per individual due to the experimental conditions and design, we observed that the food deprived turtles had temporary strong good appetite (lasted for about 2—5 days). The good appetite periods were protracted with the increasing duration of starvation. The total feed intake of each treatment group was obviously higher than the control in the first refeeding week in spite of no statistical support. Juvenile soft-shelled turtles probably adopt the first way.

Acknowledgments:

The authors would like to thank Ms. C Huang and Ms. R Jing in our laboratory for their assistance in the work.

References:

[1] Paul A J, Paul J M, Smith R L. Compensatory growth in Alaska yellow sole, *Pleuronectes asper*, following food deprivation [J]. *J. Fish Biol.*, 1995. **46**: 442—448

[2] Hornick J L, Eenaeme V C, Gerard O, *et al*. Mechanism of reduced and compensatory growth [J]. *Domestic Animal Endocrinol*, 2000, **19**: 121—132

[3] Miglaves I, Jobling M. Effect of feeding regimens on food consumption, growth rates and tissue nucleic acid in juvenile Arctic *Charr Salvdinus*, with particular respect to compensatory growth [J]. *J. Fish Biol.*, 1989, **34**: 947—957

[4] Russell N R, Wooton R J. Appetite and growth compensation in European minnows (*Phoxinus phoxinus*) following short periods of food restriction [J]. *Environ. Biol. Fish*, 1992, **34**: 277—285

[5] Gaylord T G, Gatlin D M. Assessment of compensatory growth in channel catfish *Ictaluris punctatus R.* and associated changes in body condition indices [J]. *J. World Aqua. Soc.*, 2000, **31**: 326—336

[6] Wu L X, Dong S L, Tian X L. The compensatory growth in the Chinese shrimp (*Penaeus chinensis*) following starvation [J]. *Acta Ecology Sinica*, 2001, **21**: 452—457

[7] Zhang T J, Niu C J, Sun R Y. Preliminary study of respiration metabolism in the soft-shelled turtle (*Trionyx sinensis*) [J]. *Zool. Res.*, 1996, **12**: 147—151

[8] Niu C J, Zhang T J, Sun R Y. Food consumption and growth of Chinese soft-shelled turtle (*Pelodiscus sinensis*) in relation to body weight and water temperature [J]. *Asia. Herpetol. Res.*, 1999, **8**: 81—84

[9] Zhou X Q, Xie M X, Niu C J, *et al*. The effects of dietary vitamin C on growth, liver vitamin C and serum cortisol in stressed and unstressed juvenile soft-shelled turtles (*Pelodiscus sinensis*) [J]. *Comp. Biochem. Physiol.*, 2003, **135**: 263—270

[10] Jobling M, Christiansen J S, Jorgensen E H, *et al*. The application of X-radiography in feeding and growth studies with fish: a summary of experiments conducted on *Arctic charr* [J]. *Rev. Fish. Sci.*, 1993, **1**: 223—237

[11] Wang Y, Cui Y, Yang Y, *et al*. Compensatory growth in hybrid tilapia, *Oreochromis mossambicus Peters* × *O. niloticus L*, reared in seawater [J]. *Aquaculture*, 2000, **189**: 101—108

[12] Wieser W, Krumschnabel G, Ojwang-Okor J P. The energetics of starvation and growth after refeeding in juveniles of three cyprinid species [J]. *Environ. Biol. Fish.*, 1992, **33**: 63—71

[13] McCarthy I D, Carter C G, Houlihan D F. The effect of feeding hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss* (Walbaum) [J]. *J. Fish Biol.*, 1992, **41**: 257—263

[14] Jobling M, Arnesen A M, Baardvik B M, *et al*. Monitoring feeding behaviour and food intake: methods and applications [J]. *Aqua. Nutr.*, 1995, **1**: 131—143

[15] Jobling M, Koskela J. Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth [J]. *J. Fish Biol.*, 1996, **43**: 409—419

[16] Ryer C H, Olla B L. Growth dispensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size [J]. *J. Fish Biol.*, 1996, **48**: 686—694

[17] Johansen S J S, Ekli M, Stangnes B, *et al*. Weight gain and lipid deposition in Atlantic salmon, *Salmo salar*, during compensatory growth: evidence for liposatic regulation [J]? *Aqua. Res.*, 2001, **32**: 963—974

[18] Maddock D M, Burton M P M. Some effects of starvation on the lipid and skeletal muscle layers of the winter flounder, *Pleuronectes americanus* [J]. *Can. J. Zool.*, 1994, **72**: 1672—1679

[19] Stirling H P. Effects of experimental feeding and starvation on the proximate composition of the European bass, *Picentrarchus labrax* [J]. *Mar. Biol.*, 1976, **34**: 85—91

完全或部分的食物剥夺对中华鳖(*Pelodiscus sinensis*)幼体补偿生长反应的影响: 生长率的时间变化模式与体组成的变化

颉志刚　牛翠娟

(北京师范大学生命科学学院, 生物多样性与生物工程教育部重点实验室, 北京　100875)

摘要: 为了探究中华鳖(*Pelodiscus sinensis*)幼体的补偿生长能力, 我们对中华鳖幼鳖(平均湿重9.56g)进行如下6种处理: 饥饿0(对照)、1、2、3、4周, 或者食物限制4周, 即只投喂体湿重百分之一的食物; 然后对各组进行饱食处理直到10周的实验结束为止。结果发现在饱食期的第一周各饥饿处理组的特殊生长率均显著高于对照组($p < 0.05$), 但是终体重均没有赶上对照组。当饥饿或食物限制结束时, 脂肪含量随着饥饿期的延长而降低, 灰分和水分则表现出相反的变化趋势: 脂肪含量显著低于对照($p < 0.05$), 而灰分和水分则显著高于对照($p < 0.05$)。蛋白含量则没有显著变化($p > 0.05$)。实验结束时, 除了灰分外($p < 0.05$), 其他个体组成指标均恢复到对照组的水平。以上结果表明中华鳖幼体在饥饿胁迫下首先利用脂肪作为主要能源以维持生存, 以及在该研究条件下完全的食物剥夺可以诱发其部分补偿生长反应, 而部分食物剥夺则不能诱发此反应。

关键词: 中华鳖; *Pelodiscus sinensis*; 补偿生长; 饥饿; 体组成