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High-temperature and starvation tolerances of juvenile Japanese Spanish mackerel *Scomberomorus niphonius*

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Abstract

Japanese Spanish mackerel *Scomberomorus niphonius* is a target species for stocking, but their biological characteristics at the juvenile stage are not well understood. Here, we investigated the high-temperature and starvation tolerances of hatchery-reared juveniles in captivity. We used juveniles of approximately 40 mm standard length, which was the size of the juveniles released into the field. The upper incipient lethal temperature (50% lethal water temperature) was estimated to be 31.8 °C, which was higher than the maximum sea surface temperature in the field (approximately 29 °C). The critical thermal maximum was 34.8 °C, whereas it was 36.1 °C when juveniles were preliminarily acclimated to 31 °C for 24 h. Juveniles died from 3 to 11 days under non-feeding conditions at 20 °C, whereas they died at 27 °C from 2 to 7 days. This information is expected to contribute to the development of the production of juvenile Japanese Spanish mackerel.

Keywords: Coastal habitat; Global warming; Starvation mortality; Stock enhancement; Temperature tolerance

Introduction

Water temperature is an important factor that regulates the growth rate and habitat of fish. As the water temperature of oceans has increased due to global warming, understanding the high temperature tolerance of each species is essential for predicting the responses of fish communities (Mora and Ospína 2001; Vinagre et al. 2013; Tsuchida et al. 2018). In addition, the starvation tolerance would be reduced under high-temperature conditions (Mushiake and Sekiya 1993), indicating that the indirect effects of a temperature rise on fish species with low starvation tolerance are of concern.

Japanese Spanish mackerel *Scomberomorus niphonius* is an important species for coastal fisheries in Japan. In the Seto Inland Sea, the catch and stock decreased drastically in the latter half of the 1980s. For the recovery of stock, the release of hatchery-reared juveniles as a stock enhancement program was implemented from 1998 to 2020, in association with shortening the fishing season and expanding the mesh size of the fishing gear (such as drift nets) from 2002 (Kobayashi 2003). High recapture rates of 8–16% were observed for juveniles released at 100 mm total length in 2002 and 2003 (Obata et al. 2008). The stock increased from 710 tons in 1998 to 7,065 tons in 2015 (Ishida and Katamachi 2020).

To produce juveniles, the larvae and juveniles are fed eight to ten times per day under the assumption that they have low starvation tolerance. In fact, larval Japanese Spanish mackerel are susceptible to starvation and their point of no return is ≤1 day (Shoji et al. 2002). Larvae of Japanese Spanish mackerel are piscivorous from the first feeding (Shoji and Tanaka 2001; 2004), and live hatched larvae of red seabream *Pagrus major* are supplied an initial food. Because Japanese Spanish mackerel grows rapidly and the amount of live larval red seabream can become insufficient, thawed frozen larvae with larger body sizes are supplied from 10 days after hatching (DAH). The continuous supply of thawed frozen larvae is necessary for at least several days, because it is essential for Japanese Spanish mackerel to learn that these are food because they do not feed on thawed frozen larvae after the food falls to the bottom. Supplying thawed larval food eight to ten times per day is implemented thereafter, but much labor is needed for food preparation and the removal of any remaining food, especially as the large amount of remaining food can affect the water quality if it is not removed.

Hatchery-reared juveniles of approximately 40 mm total length are released into the field, or further raised in large net cages up to a total length of 100 mm (Obata et al. 2007). Providing information on the starvation tolerance of juveniles would contribute to the efficient culture of Japanese Spanish mackerel and estimations of the duration they can survive without feeding after release. Because starvation is affected by water temperature, the responses of juveniles to high temperatures should be understood to predict post-release survival under rising temperatures caused by global warming. However, there have been no experimental studies on the temperature or starvation tolerances of juvenile Scombridae, such as Japanese Spanish mackerel. Some field studies have been conducted on the relationship between feeding, growth, and water temperature in the larvae and juveniles of wild chub mackerel *Scomber japonicus* (Taga et al. 2019) and Atlantic mackerel *Scomber scombrus* (Robert et al. 2009), and estimates of the temperature tolerance of wild tuna *Thunnus* spp. have been based on the temperature ranges in which they were observed (Boyce et al. 2008).

This study aimed to elucidate the tolerances of juvenile Japanese Spanish mackerel to high temperatures and starvation in captivity. We conducted laboratory experiments using hatchery-reared juveniles. The high-temperature tolerance of Japanese Spanish mackerel was evaluated using the following two indicators; the upper incipient lethal temperature (UILT) is 50% lethal water temperature at static temperatures (Fry et al. 1946; Jobling 1981), and the critical thermal maximum (CTMax), which is the temperature at which fish lose their ability to maintain equilibrium when the water temperature is raised at a constant rate (Becker and

Genoway 1979; Jobling 1981; Bennett and Judd 1992). Temperature tolerance is known to be influenced by previously experienced water temperatures, and fish acclimatized to high temperatures show greater tolerance to high temperatures (Reynolds and Casterlin 1979; Jobling 1981; Sakurai et al. 2021). Therefore, the CTMax was examined for juveniles kept at a natural temperature of 22 °C or those acclimatized to a high temperature of 31 °C. The starvation tolerance was examined under unfed conditions at two water temperatures of 20 °C and 27 °C, which are close to the natural sea surface temperature at the timing of release and the maximum sea surface temperature in the field in summer, respectively.

Materials and Methods

Hatchery-reared juvenile Japanese Spanish mackerel were produced at the Yashima Station, Fisheries Research and Education Agency (34° 22' N, 134° 7' E), from May to June 2020. For the juvenile production, adult Japanese Spanish mackerel (21 male fish of 595–829 mm in fork length and 22 female fish of 768–1,018 mm) were caught by the drift net fishery in the Seto Inland Sea (Harima-Nada, around Shodoshima Island, 34° N, 134°E) on May 7 or 8, 2020. Eggs were obtained by strip spawning and artificially fertilized. Hatched larvae were accommodated in a 200 kL tank and were fed with live hatched larvae of red seabream, thawed frozen larval sandlance *Ammodytes japonicus*, or thawed frozen larval Japanese anchovy *Engraulis japonicus* with additional vitamins under natural water temperature conditions. Approximately 200 juveniles (24 DAH, 37.4 ± 5.0 mm standard length [SL], 0.51 ± 0.17 g body wet weight [BW]; mean ± SD, 32 individuals sampled) were transferred to a 500 L tank filled with running natural seawater (21.5 °C) for the experiments on June 4, 2020. Before the experiments, thawed frozen larval Japanese anchovy were fed to juveniles six times a day (every 2 h from 7:00 to 17:00). Throw-in-type heaters (boilers) and chillers (AZ-

151X-15L1, Iwaki Co., Ltd., Tokyo, Japan) were used to adjust the water temperature in each experiment.

All experiments were conducted in accordance with the guidelines of the Hiroshima University Animal Research Committee (registration number 017A191002).

Experiments on high temperature tolerance

Two experiments, a 24-h survival experiment and a temperature-raising experiment, were conducted from June 6 (26 DAH) to investigate the UILT and CTMax, respectively.

In the 24-h experiment, juveniles were accommodated in 500 L tanks with temperatures of 31 °C, 32 °C, or 33 °C. These temperatures were selected based on preliminary observations that juveniles actively foraged at 29 °C with no mortality. We used 20 individuals at each temperature. To reduce the impact of rapid changes in temperature, fish were first placed in a tank filled with seawater at 25 °C, and the temperature was raised to the final desired temperatures at a rate of 3 °C h^{-1}. After reaching each target temperature, the experiment was started for 24 h in a closed water system with sufficient aeration. No food was supplied. Survival was recorded six to eight times during the 24 h experiment, and dead juveniles were removed from the tank at each observation to maintain the water quality. The SLs of dead juveniles were measured using a digital caliper. After 24 h, all dead and surviving juveniles were collected and their SL was measured, except for survivors at 31 °C; the SLs of survivors at 31 °C were measured in the later experiment. The SLs of juveniles were 40.3 ± 4.3 mm (mean ± SD), 37.3 ± 3.7 mm, and 36.4 ± 4.3 mm at 31, 32, and 33 °C, respectively. The size of the individuals was assumed to be constant during the experiment. A significant difference in SL was observed between 31 and 33 °C (Tukey-Kramer test, 31 °C vs. 32 °C: $p = 0.075$; 31 °C vs. 33 °C: $p = 0.012$; 32 °C vs. 33 °C: $p = 0.74$). Cannibalism was not observed. The water temperature during the experimental period was 30.97 ± 0.37 °C (mean ± SD), 31.85 ± 0.26 °C, and 32.90 ± 0.28 °C for the 31, 32, and 33 °C treatments, respectively.

The temperature-raising experiment was conducted using fish from different treatment groups. For the control (non-acclimation) group, 36 well-fed juveniles of 38.3 ± 4.5 mm SL (mean ± SD) were accommodated in a 500 L tank at a natural water temperature (21.3 °C) and the water temperature was raised to 30 °C over 19 h without feeding. For the acclimation group, 18 fish of 41.0 ± 4.0 mm SL that survived the 24-hour experiment at 31 °C were directly transferred to a 500 L tank with the water temperature at 30 °C. The water temperature was raised at a rate of 2 °C h^{-1} from 30 °C. Both the conditions of the juveniles and the water temperature were observed continuously, and the individuals that lost their equilibrium were collected. After the measurement of the SL, each collected individual was transferred to another tank with natural seawater and released into the sea after its recovery. Cannibalism was not observed in either group. The temperature was raised until all the individuals lost equilibrium. Food was not supplied during the experiments.

Experiments on starvation tolerance

The starvation tolerance of juveniles was examined at 20 °C and 27 °C. On June 6 (26 DAH), 18 juveniles of 38.0 ± 3.9 mm SL (mean ± SD) and 15 juveniles of 38.8 ± 3.6 mm SL were accommodated in each 100 L tank with a flow-through supply of seawater at 20 °C and 27 °C, respectively. The juveniles were reared without feeding. In the 27 °C tank, the water temperature was raised from 21 °C to 27 °C at a rate of 3 °C h^{-1}. Both tanks received flow-through seawater adjusted to each temperature at a rate of 10 mL s^{-1}, and the temperature was monitored once per day. The survival of juveniles was recorded once a day until all the individuals died. Dead individuals were collected and the SL and BW were measured. The

BW was not measured for severely damaged individuals (one individual at 20 °C and four individuals at 27 °C). Cannibalism was not observed during the experiment. The water temperature was 20.74 ± 0.37 °C (mean ± SD) and 27.22 ± 0.36 °C in the tanks at 20 °C and 27 °C, respectively.

Analyses

The following analyses were performed for the high-temperature tolerance experiments. To determine the UILT, the number of individuals who died and survived at the end of the 24-h experiment were analyzed using a generalized linear model (GLM) with a binomial distribution and logit-link function. The explanatory variable was the average water temperature, the model selection was performed based on the Akaike information criterion (AIC), and the model with the lowest AIC was selected. Preliminarily, individual SL was excluded in the selected individual-based GLM for death or survival, although this model was not used because of pseudo-replication.

To determine the CTMax, the temperature at which each individual lost its equilibrium was averaged for each of the control and acclimation groups. A linear model was constructed for individual data using the SL and group as initial explanatory variables. The SL was excluded, and the group was adopted as an explanatory variable based on the AIC.

Another GLM with a binomial distribution and logit-link function was constructed for the death or survival of each individual in the starvation experiment. The average water temperature, SL, and starved days were used as initial explanatory variables, and the model was selected based on the AIC. All analyses were performed using R software version 3.5.1 (www.r-project.org).

The survival activity index (SAI), which has been used to evaluate the starvation tolerance of fish larvae (Shimma and Tsujigado 1981; Matsuo et al. 2006), was calculated using the following formula:

$$SAI = \frac{1}{N}\sum_{i=1}^{m}(N - hi) \times i$$

where *N* is the total number of individuals, *hi* is the cumulative number of dead individuals by the *i*-th day, and m is the number of days until all individuals die of starvation.

To assess the somatic condition of the dead individuals, the condition factor (*K*) was evaluated using the following formula:

$$K = BW \times SL^{-3} \times 10^{6}$$

Results

High temperature tolerance

The UILT was estimated to be 31.8 °C from the 24-h experiment (Fig. 1). Dead individuals were observed at all experimental temperatures (31, 32, and 33 °C). One individual died within 16 h and another within 18 h after the onset of the experiment at 31 °C (Online Resource, Fig. S1), and the ultimate mortality rate was 10% at this temperature. At 32 °C, one individual died within 1 h and another 10 individuals died within 16 h after the onset of the experiment, and the ultimate mortality rate was 55%. At 33 °C, nine individuals died within 1 h and another nine individuals died within 16 h after the onset of the experiment, and the ultimate mortality was 90%. In the GLM for mortality, water temperature was adopted as the explanatory variable (Table 1).

The average CTMax was 34.81 °C and 36.07 °C in the control and acclimation groups, respectively, in the temperature raising experiment (Fig. 2). In the control group, one individual lost its equilibrium at 33.9 °C, and all remaining juveniles lost their equilibrium by the time the temperature reached 35.6 °C (Online Resource, Fig. S2). In the acclimation group, one individual lost its equilibrium at 34.9 °C, and all remaining juveniles lost their equilibrium by the time the temperature reached 36.5 °C.

Starvation tolerance

The first dead individual was observed on the fourth day of starvation at 20 °C, whereas at 27 °C a dead individual was observed on the second day of starvation (Online Resource, Fig. S3). The mortality rate reached 50% on the eighth and fifth days at 20 °C and 27 °C, respectively. The average duration until death was 7.7 and 4.8 days at 20 °C and 27 °C, respectively, and it took 11 and 7 days until all individuals died at these respective temperatures. The K values of the dead individuals (20 °C: $N = 14$, $K = 5.27 \pm 0.79$; 27 °C: $N = 14$, $K = 5.24 \pm 1.01$; mean ± SD) were smaller on later days (Fig. 4). The K of the individuals who died at 20 °C was 7.64 on the fourth day and 5.92–4.25 from the fifth day to the eleventh day. The K at 27 °C was 7.05–5.79 on the third day and 6.12–3.50 from the fourth day to the seventh day. The K of dead individuals ≥38 mm SL was <6 (Fig. 4).

In the GLM for mortality, the water temperature, SL, and number of starved days were all adopted as explanatory variables (Table 1). According to the model, mortality was greater with higher temperatures, smaller individuals, and more starved days (Fig. 3). The number of days of starvation for 50% mortality in juveniles at 30 mm, 40 mm, and 50 mm SL, estimated from the model, were 6.7, 8.5, and 10.4 days at 20 °C and 3.3, 5.2, and 7.0 days at 27 °C, respectively. The SAI was 27.6 and 9.9 at 20 °C and 27 °C, respectively.

Discussion

This study is noteworthy as the first report on the high-temperature and starvation tolerances of juvenile Scombridae. Juvenile Japanese Spanish mackerel have sufficient high-temperature tolerance for survival in the Seto Inland Sea, where the highest sea surface temperature recorded until 2002 or 2003 was approximately 29 °C in September (Yamamoto 2003; Wanishi 2004). Juveniles were released in the field in June when sea surface temperatures were around 20 °C, indicating that the immediate limitation of the distribution of juveniles due to future temperature increases is unlikely. However, the indirect effects of rising temperatures on the post-release survival or distribution of wild juveniles may be of concern because the starvation tolerance is reduced at higher temperatures. Because the sea surface temperature may exceed 30 °C in the future, further investigation of the impact of higher temperatures on the distribution of Japanese Spanish mackerel is necessary.

The average CTMax of juveniles without acclimation to high temperatures was 34.8 °C, whereas juveniles acclimated to 31 °C for 24 h exhibited a 1.3 °C higher CTMax. It was demonstrated that only 24 h of acclimation can affect the CTMax, whereas past studies revealed acclimation effects by previous exposures to high temperatures for more than two weeks were required for increasing the high-temperature tolerance (Reynolds and Casterlin 1979; Becker and Genoway 1979).

Under starvation conditions, it took 11 days until all juveniles died at 20 °C. This result clearly showed that juveniles have a greater starvation tolerance than larvae, which cannot tolerate 1 day of starvation after yolk absorption by 9 DAH under unfed conditions at 18.5 °C and 20 °C (Shoji et al. 2002). The average number of days until the death of juvenile Japanese Spanish mackerel was 7.7 days at 20 °C. Similar information has been reported for juvenile Japanese flounder *Paralichthys olivaceus* of 23–26 mm SL at 21–24 °C (13.6 days; Tanda 1989), juvenile red sea bream of 40 mm SL at 19–25 °C (26 days for 50% mortality; Umino et al. 1991), juvenile Atlantic silverside *Menidia menidia* of <30 mm total length at 24 °C (approximately 9 days for 50% mortality; Baumann et al. 2018), and juvenile coral trout *Plectropomus leopardus* of 50 mm SL at 28 °C (59 days; Hamasaki et al. 2003). Although the size, temperature, or taxonomic group largely differed between these studies, the comparative starvation tolerance of juvenile Japanese Spanish mackerel seemed to be relatively low. In addition, the days until death and SAI were smaller at 27 °C than at 20°C, suggesting that a higher water temperature leads to a lower starvation tolerance of juveniles. This is presumably due to active metabolism at high water temperatures (Yamamoto 1989; Kawabe 2003). The SAI has been used to evaluate the activity of larvae under unfed conditions (Shimma and Tsujigado 1981; Mushiake and Sekiya 1993), but it has seldom been used for juveniles. The SAI of juvenile Japanese Spanish mackerel should be compared with that of other scombrid species in the future.

The average condition factor *K* of the dead fish in the starvation experiment was 5.3, whereas the average condition factor of live fish under feeding conditions before the experiment on June 4, 2020 was 9.5. This result indicated that a body weight of approximately 56% of the normally fed individuals is critical for the survival of juvenile Japanese Spanish mackerel. This value is higher than 50% in juvenile Japanese flounder (Tanda 1989) or 46–50% in juvenile coral trout (Hamasaki et al. 2003), indicating a relatively low starvation tolerance in juvenile Japanese Spanish mackerel. Higher condition factors can contribute to a higher temperature tolerance (Baker and Heidinger 1996), indicating that maintaining high condition factors in juveniles leads to greater tolerance to both high temperatures and starvation. Thus, monitoring the condition factor will provide important information on the optimal feeding frequency and efficient culture of juvenile Japanese Spanish mackerel.

This study demonstrated that juvenile Japanese Spanish mackerel greatly developed their tolerance to starvation compared with those in the larval stage. This finding is expected to contribute to the efficient juvenile production of Japanese Spanish mackerel for stocking. The production of juvenile Japanese Spanish mackerel usually takes one month. For example, Japanese Spanish mackerel grew to >70 mm total length at 34 DAH (Hayashi et al. 2009). Feeding juveniles several times a day for several days after shifting the food from live hatched larval red seabream to thawed frozen larval sandlance or anchovy is necessary for teaching the juveniles, but the frequency of feeding can be reduced gradually by taking the starvation tolerance of the juveniles into account. However, it should be confirmed that reducing the food supply does not promote cannibalism in Japanese Spanish mackerel.

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Table 1 Results of the generalized linear model (binomial family and logit link) for the death/survival of juvenile Japanese Spanish mackerel in the laboratory experiments

Analysis of deviance				Summary			
Error source	df	LR chisq	*p*	Parameter	Estimate	SE	*p*
24-h experiment for UILT (Residual deviance = 0.32, df = 2)							
				Intercept	–72.51	17.52	<0.001
WT	1	29.25	<0.001	WT	2.28	0.55	<0.001
Starvation experiment (Residual deviance = 114.06, df = 168)							
				Intercept	–1.11	2.54	0.66
WT	1	26.94	<0.001	WT (27 °C)*	3.35	0.77	<0.001
SL	1	7.35	0.007	SL	–0.19	0.07	0.011
Days	1	53.03	<0.001	Days	1.00	0.18	<0.001

The analysis of deviance was carried out using Type II likelihood ratio chi-square (LR Chisq) tests. The response variable was the death or survival of each individual. The initial explanatory variables were water temperature (WT), standard length (SL) of each individual, and days under non-feeding conditions (days) for the starvation experiment. The final model was selected based on the Akaike information criterion. UILT: upper incipient lethal temperature; df: degrees of freedom; SE: standard error.

*The effect of temperature in the starvation experiment was assessed based on the temperature of 20 °C.

Figure legends

Fig. 1. Relationship between the water temperature and mortality of juvenile Japanese Spanish mackerel in the 24-h experiment at 31, 32, and 33 °C. The line shows the prediction by the generalized linear model. Shaded areas show 95% confidence intervals.

Fig. 2. Boxplots of the critical thermal maximum (CTMax) of juvenile Japanese Spanish mackerel in the rising temperature experiment. Boxes show the 25% and 75% quartiles and the median, dashed vertical bars show the maximum and minimum values, solid triangles show the mean values, and open circles show outliers. For the acclimation group, juveniles were acclimated to 31 °C for 24 h prior to the experiment. The control group was not acclimated.

Fig. 3. Mortality probability of juvenile Japanese Spanish mackerel of each size (standard length) in relation to the starvation period under two temperatures. Solid and dashed lines represent mortality at 20 °C and 27 °C, respectively, as predicted using the generalized linear model. Shaded areas show the 95% confidence intervals.

Fig. 4. Condition factor of dead individuals of juvenile Japanese Spanish mackerel in relation to the number of days of starvation (upper panel) or the standard length of juveniles (lower panel) in the starvation experiment.

Figure1

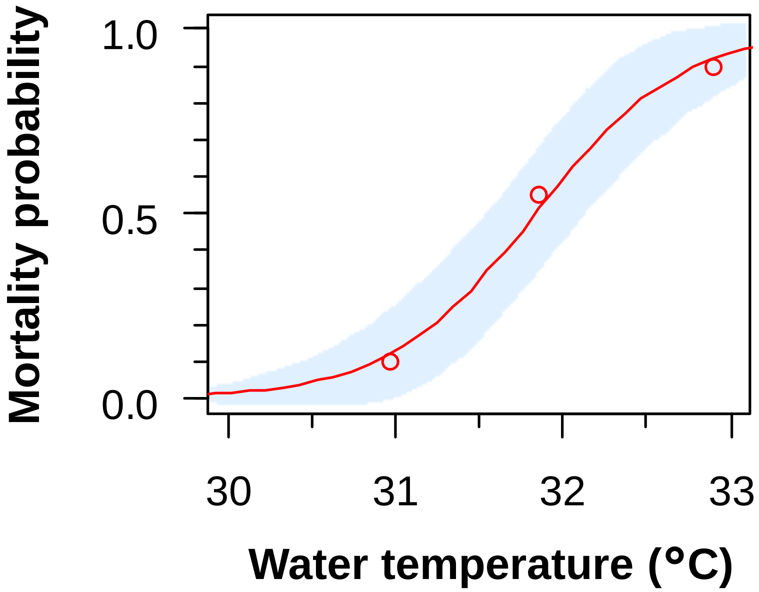

Mortality probability
1.0
0.5
0.0
30
31
32
33
Water temperature (°C)

Figure2

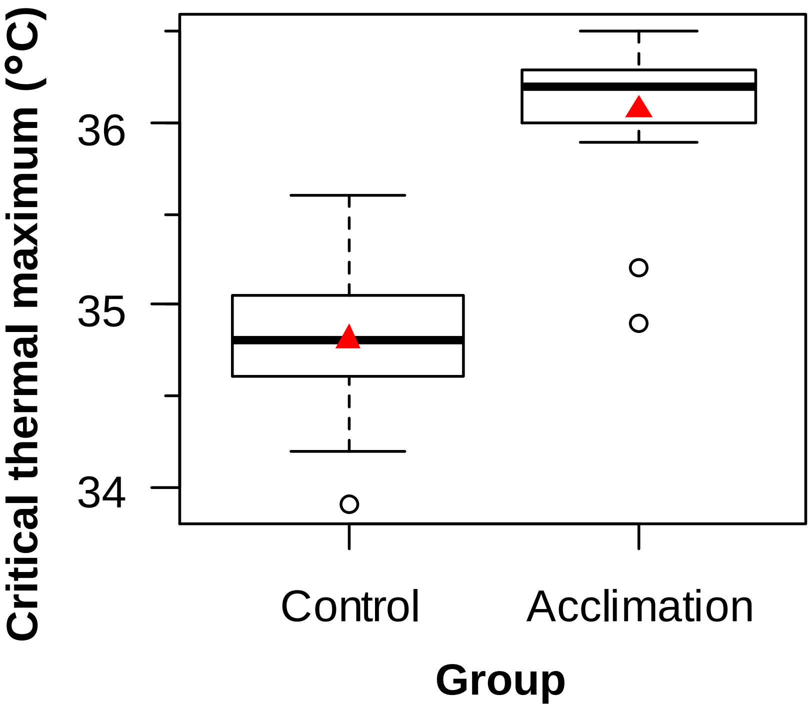
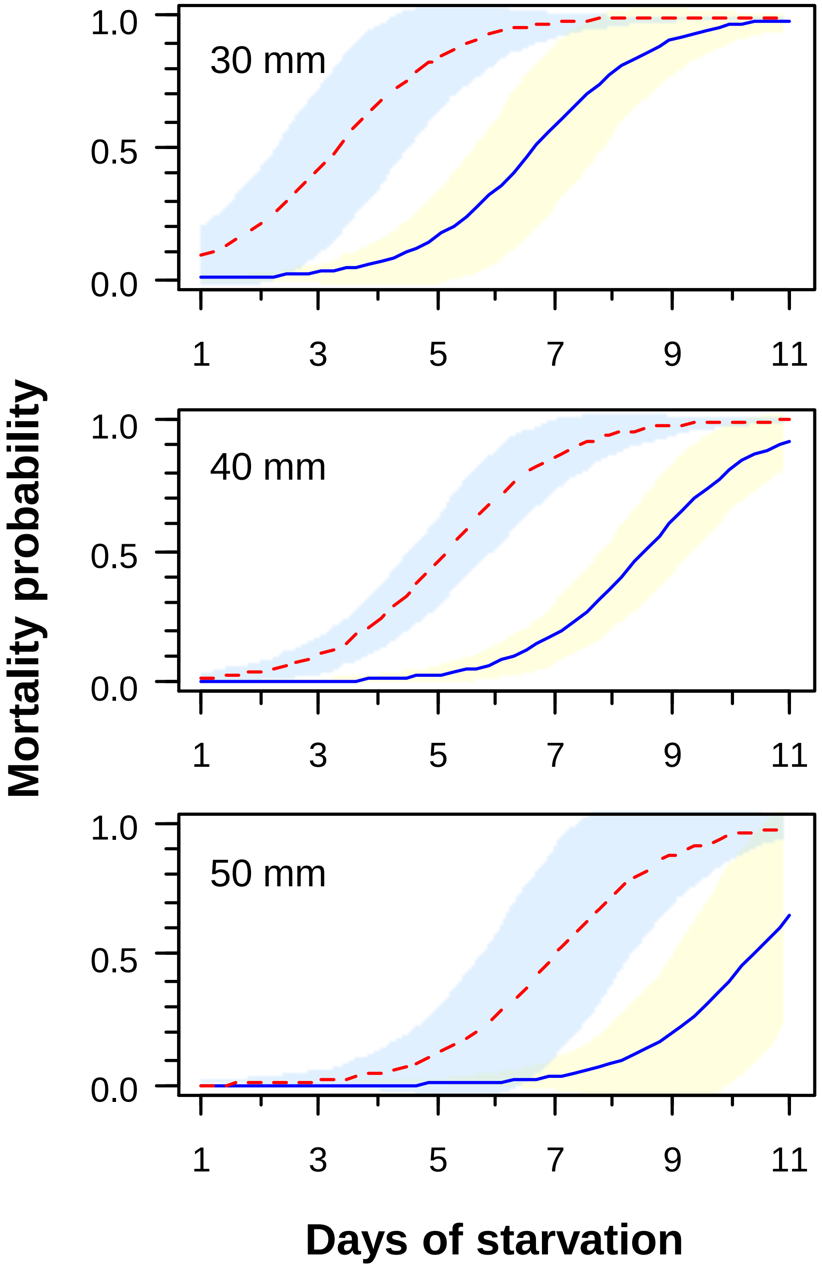
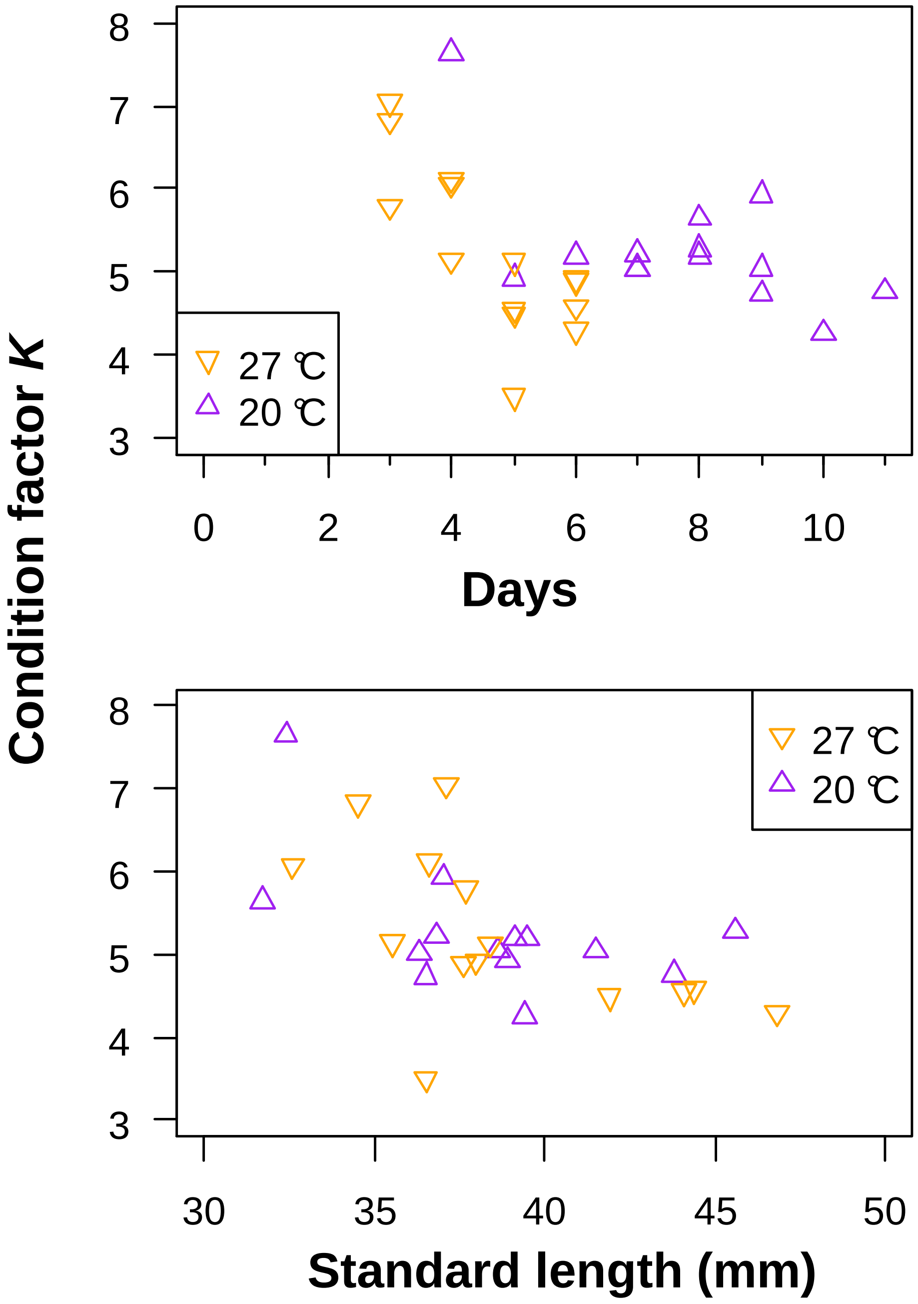

Critical thermal maximum (°C)
36
35
34
Control
Acclimation
Group

Figure3



30 mm
40 mm
50 mm
1.0
0.5
0.0
1
3
5
7
9
11
Mortality probability
Days of starvation

Figure4



Condition factor *K*
8
7
6
5
4
3
0
2
4
6
8
10
Days
▽ 27 ℃
△ 20 ℃
8
7
6
5
4
3
30
35
40
45
50
Standard length (mm)
▽ 27 ℃
△ 20 ℃