Influence of temperature and salinity on length and yolk utilization of striped bass larvae

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The effects of temperature and salinity on yolk utilization and growth of larval striped bass (*Morone saxatilis*) from Canadian maritime stocks were studied to determine optimal rearing conditions. Larval length increased during yolk utilization and maximum length (L_{max}) was attained at about 70 degree-days post-hatch. Dry weight declined during yolk utilization, whereas, larval wet weight was relatively constant and only declined when yolk was depleted. Temperature and salinity significantly affected the L_{max} . Temperatures exceeding 18°C resulted in lower L_{max} . Higher L_{max} values were attained at 5 % than at 1 or 10 %. Time to reach L_{max} was longer at 5 and 10 % than at 1 % for any experimental temperature. Time to reach L_{max} was 3 days post-hatch longer than times to maximum embryo dry weight. The Q_{10} of yolk utilization was 1.71, 1.53 and 2.52 at 1, 5 and 10 %, respectively. Times to terminal yolk utilization indicated rapid development of locomotory and predatory capabilities. These and other developmental strategies were compared to those of salmonids. Rearing striped bass larvae at 14–16°C and 5 % throughout yolk utilization should result in longer larvae at initial first feeding.

KEYWORDS: Salinity, Striped bass (Morone saxatilis), Temperature, Yolk utilization

INTRODUCTION

The striped bass (*Morone saxatilis* Walbaum) is an anadromous species with a natural range in eastern North America, extending from Florida, USA, to northern New Brunswick, Canada (historically to the St. Lawrence River) (Melvin, 1991). In the Canadian Maritime Provinces, spawning typically occurs at head of tide in water of negligible salinity during the first 2 weeks in June (Melvin, 1991). As a result of several influences (success culturing striped bass in the US, the success of the salmon aquaculture industry in eastern Canada, and the decline of local striped bass stocks), there has been some interest in striped bass as an aquaculture species in Atlantic Canada – particularly in areas where sea surface temperatures in summer are too warm for salmon culture. Accordingly, the authors have been assessing the influence of environmental factors on growth rates of the various stages of local



FIG. 1. A proposed general model of larval fish yolk utilization. Yolk utilization is postulated to be linear. A representative growth function increases during yolk resorption to a maximum (f_{max}), then declines.

stocks. This paper deals with the dynamics of larval yolk utilization and growth prior to exogenous feeding at several experimental temperatures and salinities.

Striped bass larval development in the laboratory has been the subject of a number of studies, dating back to that of Doroshev (1970). The time from fertilization to first feeding is very short in striped bass – in the order of 6–10 days (Doroshev, 1970; Rogers and Westin, 1981; Eldridge *et al.*, 1982; Tsai, 1991). The endogenous food reserves of prefeeding larvae consist of yolk (primarily protein) and an oil droplet (mainly steryl and wax esters) (Eldridge *et al.*, 1983). Findings differ on the relative rates of usage of these two endogenous sources of energy. Eldridge *et al.* (1982) found that much of the oil droplet tends to be conserved until 20–30 days post-fertilization (dpf), with yolk utilization completed by day 6–7, at which point exogenous feeding began (at 18° C). Similar results were obtained by Rogers and Westin (1981). Other publications indicate more similar rates of oil and yolk utilization (e.g. Doroshev, 1970), with the oil supply lasting only 3–4 days beyond terminal yolk utilization at 17–18°C.

In developing culture techniques, it seems desirable to adopt an environmental regimen which maximizes efficiency of utilization of energy reserves, resulting in the largest possible first-feeding larvae. Larger size at transitional periods, such as first-feeding is generally considered desirable from the point of view of minimizing mortalities and maximizing initial feeding success (e.g., Hansen, 1985). This paper investigates the influence of two environmental variables, temperature and salinity, on the yolk utilization phase of striped bass larvae. Generally speaking, striped bass yolk-sac larvae have been found to survive best at temperatures of 15–20°C and

salinities of 1-5 % (Albrecht, 1964; Doroshev, 1970; Lal *et al.*, 1977; Morgan *et al.*, 1981; Hall, 1991). Two questions are addressed: how do temperature and salinity affect yolk utilization and larval size; and how do several parameters of larval development, such as maximal larval length, relate to generally accepted times to first feeding?

A simple model of larval development during yolk utilization as a framework for planning and interpreting experiments (Fig. 1) is used. Yolk is consumed linearly with time. A fraction of the utilized yolk is converted to embryonic mass as indicated by the growth curve in the figure, until the yolk is depleted. Embryonic mass then declines through starvation and metabolic breakdown of embryonic tissue. This general model has been shown to accurately portray salmonid larval development in many studies (e.g. Heming, 1982; Hansen and Møller, 1985; Peterson and Martin-Robichaud, 1995). It is of interest to see if the model is applicable to larval development of species with a very different reproductive strategy.

MATERIALS AND METHODS

Experiments were performed in June 1992 using fertilized eggs from tank-spawned broodstock of Stewiacke River, Nova Scotia, origin. Broodstock were brought into spawning condition by manipulation of temperature, salinity and photoperiod (Peterson, 1991). Oviduct catheterization and ovarian biopsies were performed on females prior to spawning induction to ensure that oocytes had developed to the proper stage (Rees and Harrell, 1990). Males were running ripe at least a month before spawning, and continued to be so throughout the spawning period. Broodstock were induced to spawn by insertion of slow-release GnRH implants (Repro BoostTM, Aquapharm Technologies Corp.) into the dorsal musculature. The GnRH dosage was 50 and 30 μ g/kg for females and males, respectively. After implant insertion, the broodstock routinely spawned in the holding tanks within 36h. Broodstock sizes ranged from 4–8 kg.

Striped bass were tank-spawned with three females and two males in the tank. This group of fish had been kept together for 4y, and this was the third time they spawned in captivity. From observations during spawning, it is believed (although it cannot be certain) that all fish participated in spawning. Fertilization rate was over 90% and early development of all eggs was in synchrony. The fact that the experimental eggs and larvae may have derived from three females may have resulted in some increase in experimental variability. The spawning tank was of 2 m diameter and 1.5 m depth.

After spawning, newly fertilized eggs (less than 1h after spawning) were transferred to 1 m circular tanks and maintained at 15° C and 3.5 % salinity until hatch. At 50% hatch (2 days post-fertilization), 204(3) newly hatched larvae or eggs soon to hatch were transferred to 21 chambers (Fig. 2) provided with a continuous upwelling and circumferential water flow (based on a design by Hughes *et al.*, 1974).

Three salinities, 1, 5 and 10 %, and five temperatures, 14, 16, 18, 20 and 22°C, were tested. Plexiglass header tanks, partitioned linearly into 10 chambers, were used to alternately heat and aerate water of the appropriate salinity with thermostatically controlled immersion heaters. Flow rates to the chambers were 188(22) ml min⁻¹.



FIG. 2. Diagrams of top (A) and side (B) views of the experimental chambers for rearing larval striped bass.

Temperatures, salinities and flows were measured daily. Length, and wet and dry weight determinations were done on samples of 10 fresh larvae from each treatment at least once during the experiment to compare with similar measurements on preserved larvae, which were sampled daily from each treatment. The rapid development of the larvae necessitated the use of preserved larvae for analyses. The larvae that were to be measured fresh were collected by pipette and placed into water of identical salinity containing MS 222 to immobilize them. Measurements were as for preserved larvae, except that rinsing was unnecessary and yolk could not be separated from the embryo. Larvae to be preserved were rinsed in 5% buffered formalin prior to storage in this solution. Sampling was continued for 14 days post-hatch. The preserved larvae were rinsed in refrigerated distilled water 12h prior to dissection. A larva to be dissected was placed on a pre-weighed square (ca. 7 mm on a side, with corners turned up) of heavy aluminium foil (cut from aluminium weighing pans). The total lengths of 10 larvae from each treatment were estimated with an ocular micrometer ($64 \times$ magnification) at ± 0.05 mm. The foil plus larva was placed on a temperature-controlled microscope stage (Servo-tek TS-4 controller). The temperature of the stage was set at the dew point of the laboratory air at the time to eliminate either water loss through evaporation or gain through condensation. Most measurements were made on formalin-fixed material, but a series of fresh larvae was processed to compare with preserved specimens. Excess moisture was removed with the point of a triangle cut out of filter paper. Cutting of the filter paper to a fine point was necessary to prevent adherence of the larva to the paper. For five larvae from each treatment, the undissected larva was weighed on an electrobalance to the nearest μg . To correct for loss of moisture during the weighing process, the wet weight – when desired – was recorded at 10s intervals for 30s from the time the pan was removed from the microscope stage. The weight at

zero time was determined by linear extrapolation. The dry weights were determined after drying at 60°C for at least 48h in Petrie dishes covered with filter paper to occlude dust.

Five larvae for each treatment were dissected into embryo, yolk pellet and oil components as follows. The yolk sac was opened using stainless steel microelectrodes as dissecting instruments. The yolk pellet, which hardened during formalin fixation, was teased out, rolled on the weighing pan to minimize adherent oil, transferred to a separate pre-weighed pan, then placed in a Petrie dish for drying and weighing. The embryo was similarly freed of oil by blotting on the weighing pan and transferred to another pre-weighed pan. The oil flowed onto the pan when the yolk sac was punctured and during dissection, and was estimated as the remaining fluid on the dissection pan after removal of the yolk pellet and embryo. Statistical analyses utilized Student's t-test, regression analysis and analysis of covariance (Sokal and Rohlf, 1981).

RESULTS

Mean temperatures and salinities with standard deviations are given in Table 1. For 21 samples (larval ages ranging from 1–8 days), 10 fresh larvae were processed for comparison with 10 preserved larvae to assess the influence of preservation on larval length (Table 2). In only 2 of the 21 comparisons did the fresh and preserved lengths differ significantly (t-test, 0.05 probability). Lengths measured from preserved larvae tended to be longer than those measured from fresh larvae by 0.08 mm on average. The difference in length between fresh and preserved larvae was less the longer the larvae; the regression of preserved larval length on fresh larvae by 1.0 km a slope of 0.68, significantly different from 1.0, $R^2 = 0.7$. It was not attempted to correct preserved larval lengths to fresh, as the corrections would only change the values 1–2% and would increase the error due to addition of the error of estimation of the slope to the error of estimation of the effect of temperature and salinity, as the correction for longer larvae would be less than that for shorter larvae.

To see what parameters of striped bass development, if any, fit the proposed model, the larval wet weights, dry weights and lengths of the fresh material were plotted vs degree-days post-hatch (Fig. 3). Only larval length exhibited the proposed pattern (Fig. 3, middle panel) compared to Fig 1. Larval wet weight (Fig. 3, lower panel) showed no trend over the first 70 days post-hatch, then declined starting sometime between 70 and 176 days post-hatch. Water content remained constant throughout the yolk utilization phase. Dry weight declined over yolk utilization (Fig. 3), as expected, since no exogenous materials are absorbed and yolk conversion is not completely efficient. To examine more closely the effects of temperature and salinity treatments on larval development, larval length was thus considered the key variable. Embryo dry weight, not measured on the fresh material, was also examined.

Larval length increased for the first few days post-hatch at all treatments (Fig. 4), attained a maximum, then decreased. Parabolic regression provided a good fit of the relationship with R^2 values of 0.6–0.9. By differentiating the parabolic equations,

	Salinity														
	1 ‰					5 ‰					10 ‰				
	Temper	ature													
:	14	16	18	20	22	14	16	18	20	22	14	16	18	20	22
ů	14.9	16.3	17.4	20.0	21.7	14.6	16.0	17.7	19.1	20.3	14.2	16.1	18.9	20.6	22.5
	(0.56)	(0.76)	(0.74)	(1.47)	(1.79)	(0.63)	(1.07)	(2.60)	(2.42)	(2.91)	(0.71)	(0.83)	(1.32)	(1.22)	(2.13)
%	1.2	1.1		1.2	1.2	5.2	5.2	5.1	5.5	5.5	10.6	10.6	10.4	10.4	11.0
	(0.26)	(0.06)	(0.07)	(0.17)	(0.17)	(0.66)	(0.82)	(0.79)	(0.74)	(0.71)	(1.7)	(1.9)	(1.8)	(1.8)	(1.8)

TABLE 2. Standard lengths of fresh and preserved striped bass larvae for 18 samples from various salinities, temperatures and days post-hatch. Sample size = 10 in all cases. Asterisks indicate comparisons which were significantly different (t-test, p < 0.05).

Salinity (‰)	Temperature (°C)	Age (dph)	Fresh (SE)	Preserved (SE)
1	22	1	5.51 (0.08)	5.65 (0.03)
		8	5.75 (0.09)	5.76 (0.08)
	20	2	5.68 (0.05)	5.79 (0.03)
	18	3	5.98 (0.11)	6.11 (0.03)
	16	4	6.06 (0.08)	6.28 (0.05)
	14	5	6.15 (0.07)	6.18 (0.03)
5	22	1	5.63 (0.08)	5.67 (0.04)
		8	5.86 (0.08)	6.10 (0.04)
	20	2	5.91 (0.07)	5.88 (0.02)
	18	3	5.92 (0.07)	5.91 (0.02)
	16	4	6.16 (0.05)	6.13 (0.06)
	14	5	6.07 (0.04)	6.12 (0.05)
10	22	1	5.39 (0.07)	5.64 (0.04)*
		8	5.41 (0.05)	5.88 (0.04)*
	20	2	5.78 (0.04)	5.83 (0.05)
	18	3	6.01 (0.08)	6.00 (0.04)
	16	4	5.92 (0.08)	5.95 (0.02)
	14	5	5.86 (0.09)	5.95 (0.05)

maximum larval lengths (L_{max}) and times to attainment of maximum larval length were calculated. L_{max} values for the various salinity-temperature combinations were fitted with a quadratic response surface (Fig. 5). Both temperature and salinity had significant effects on L_{max} (2-way ANCOVA, $F_{temp} = 3.66$, p < 0.05, df < 4; $F_{sal} = 4.99$, p < 0.025, df = 2). Temperatures exceeding 18°C resulted in lower L_{max} . At any given salinity, L_{max} values were higher at 5 ‰ than at 1 or 10 ‰ salinities, resulting in an elongation of the isopleths in Fig. 5 towards higher temperatures along the 5 ‰ line. The mean standard deviation between experimental and predicted values was 0.065 mm.

The estimated times (days) to attain L_{max} (T_{max}) were also calculated from the parabolic equations (Table 3). Times to attain maximum length tended to be longer at 5 and 10 % than at 1 % for any temperature, ranging from 4.6 days at 22°C/1 % to 10.7 at 14°C/5-10 %.

For 14 of 141 samples, dry larval weights were determined from both fresh and preserved material for comparative purposes. The dry larval weights from preserved material were consistently ca. $50 \ \mu g$ lower than dry weights of equivalent fresh material (preserved dry weight (mg) = 0.05 + 1.06 fresh dry weight, $R^2 = 0.84$). In 8 of 141 samples (none from the 14 samples discussed above), oil had been released from the preserved material, resulting in dry weights well out of line with the rest of the samples. These eight samples were discarded from the analyses.



FIG. 3. Changes in dry weight (A), length (B) and wet weight (C) of larval striped bass with time after hatch, measurements based on fresh larvae from various treatments. x = 1 % salinity; $\circ = 5 \%$; $\bullet = 10 \%$.

When dissecting preserved larvae into embryonic, yolk and oil components, budgets were analysed to determine losses through dissection by summing embryo, yolk and oil dry weights, then comparing these with dry weights of undissected larvae from the same samples. The percent recovery from summing dissected components averaged 97% of the undissected dry weights, ranging from 85.1-102.3%. As with larval length, changes in embryo dry weight with time were fitted to a parabolic relationship (example in Fig. 6), although the fit was not nearly so good, with R² varying from 0.03–0.38. Undoubtedly, errors associated with dissection of embryos from yolk and oil contributed to the increased scatter in embryo dry weight data as compared to those for larval length. The increase in embryonic dry weight was small during yolk utilization – 18 µg on average (14% of



FIG. 4. Striped bass larval length as a function of time post-hatch. The curve is derived from the parabolic equation of best fit ($I = 4.57 + 0.551t - 0.0446t^2$), where I = larval length and t = time post-hatch; $R^2 = 0.89$. The dotted lines indicate the confidence limits of the regression. Each dot represents the mean of 10 measurements. Vertical bars indicate the standard error for each mean.

initial embryo dry weight), which was within the error range in determination of individual weights.

Although the fit of the embryo dry weight data to parabolic functions was poor, t_{max} values derived from the larval length curves correlated significantly with t_{max} values derived from embryonic dry weights (t_{max} (I) = 3.21 + 1.02 t(ew) (R² = 0.74), where I = length and ew = embryonic dry weight. Times to maximum larval length for any given treatment were consistently 3 days post-hatch longer than times to maximum embryo dry weight. Striped bass larvae hatched with an average of 72.2(3.65) µg of dry yolk pellet. The rates of yolk utilization at the various treatments were linear with time (Fig. 7). Temperature and salinity interacted in their influence on rates of yolk utilization (Table 4). The Q₁₀ of yolk utilization was 2.52 at 10 ‰ as compared to 1.71 and 1.53 at 1 and 5 ‰, respectively, so that the rate was considerably higher at 10 ‰ at the higher test temperatures.

Times to terminal yolk resorption were estimated from the regressions of yolk dry weight on time. Times to terminal yolk utilization were usually shorter than times to maximal larval length, by 1.2 days on average (Table 3).



FIG. 5. Isopleths of maximal striped bass larval length as a function of rearing temperature and salinity. The isopleths were derived from the regression of best fit ($L_{max} = 4.78 + 0.216T + 0.0615S - 0.0073T^2 - 0.0082S^2 + 0.0015TS$; T = temperature, S = salinity). 95% confidence limits for the measured L_{max} at each treatment are in parentheses.

Mortalities were not determined in these experiments due, in part, to the fragility of the small larvae. Of the 204 larvae placed in each treatment, 50% were sampled for analyses. In most treatments, there were many larvae left at the termination of the experiment. At 22° C and 1 % salinity, larvae died rapidly towards the end of the

TABLE 3. Comparison of times (days) to maximum larval length (t_{max}) and times to terminal yolk utilization (pellet) for various salinity-temperature treatments. Numbers in parentheses are confidence limits. Confidence limits for L_{max} are given in Fig. 5.

	1 ‰		5 ‰		10 ‰	
Temp (°C)	t _{max}	Pellet	t _{max}	Pellet	t _{max}	Pellet
14	6.2	6.7 (0.86)	10.7	6.9 (0.55)	10.7	7.3 (0.92)
16	5.8	6.3 (0.40)	7.67	5.9 (0.75)	7.5	5.5 (0.50)
18	5.0	6.2 (0.40)	6.88	5.1 (0.40)	9.3	4.2 (0.45)
20	5.3	4.9 (0.35)	5.16	5.2 (0.40)	8.2	3.6 (0.50)
22	4.6	4.2 (0.45)	5.65	4.5 (0.50)	5.0	3.6 (0.35)



FIG. 6. Striped bass embryo dry weight as a function of days post-hatch. The curve is derived from the parabolic equation of best fit ($e = 0.118 + 0.009t - 0.00127t_2$, $R^2 = 0.12$). The vertical bars indicate standard error for each mean. Each point is the mean of five measurements.

experiment due, no doubt, to lack of nutrient reserves, so that after 10 days posthatch none remained.

DISCUSSION

It is suggested that increase in larval length is a biologically important aspect of the yolk utilization phase of striped bass. It is postulated that most of this increase in length may be post-anal, reflecting the rapid development of locomotory capability. This development was very obvious when doing dissections of larvae of varying ages after hatch, but should be confirmed by appropriate measurements. In newly hatched larvae, the caudal peduncle arose near the posterior margin of the yolk sac and became increasingly separated with elongation of the post-anal trunk musculature. The other striking feature of the striped bass yolk resorption phase is the buccal development. Newly hatched larvae have no functional mouth, and jaw and buccal cavity development is rapid in the yolk sac stage. From these descriptive



FIG. 7. Yolk dry weight as a function of days post-hatch for two experimental temperatures. Lines drawn from appropriate regression equations (for 1 ‰: 14°C; p = 0.075 - 0.0113t, for 5 ‰: 14°C; p = 0.071 - 0.0103t, for 10 ‰: 14°C; p = 0.074 - 0.0101t, for 1 ‰: 22°C; P = 0.072 - 0.0172t, for 5 ‰: 22°C; p = 0.068 - 0.0152t, for 10 ‰: 22°C; p = 0.071 - 0.0198t). R² values ranged from 0.67 - 0.85.

observations, it is concluded that the striped bass yolk sac phase is one of rapid development of locomotory and predatory capacities.

In contrast to the nearly 50% increase in length during yolk resorption, increase in embryonic dry mass is only about 14%. In comparison, the Atlantic salmon (*Salmo salar*) embryo dry mass triples during yolk resorption (Peterson and Martin-Robichaud, 1995). This difference reflects the very different reproductive strategies of the two species. The salmon produces relatively few eggs with a large amount of yolk to be utilized during a lengthy yolk utilization phase in a stable sub-gravel environment. Under these conditions, somatic growth is favoured, and the quiescent larvae may achieve gross conversion efficiencies of 70–80% (Hansen and Møller, 1985). The striped bass produces many more eggs with relatively little yolk

	Temperature (°C)							
Salinity (‰)	14	16	18	20	22			
1	–11.3 (1.4)	–10.7 (0.9)	–11.8 (0.8)	-13.5 (1.2)	–17.2 (1.8)			
	33	30	29	26	13			
5	–10.3 (0.8)	–13.6 (1.6)	–13.7 (1.1)	–14.1 (1.2)	–15.2 (1.7)			
	32	25	31	27	13			
10	–10.1 (1.2)	–13.0 (1.2)	–18.6 (2.2)	–20.5 (2.4)	–19.8 (2.3)			
	36	30	12	13	18			

TABLE 4. Rates of yolk utilization of striped bass larvae (μ g/day) for various test temperatures and salinities. Numbers in parentheses are standard errors of the slopes. The bottom number in each cell is the degrees of freedom associated with each regression.

and releases them in a turbulent estuarine environment. The larvae swim continuously during the short yolk resorption phase. Under these conditions, somatic growth is minimized and gross conversion efficiency is only of the order of 25% (derived from values obtained in this study).

The model shown in Fig. 1 has found utility in salmonid culture as a predictor for first feeding, with embryo dry mass and alevin wet weight both exhibiting the proposed relationship to yolk utilization. With striped bass, embryo dry mass is a parameter of little practical value in this regard because of the relatively small increase and difficulty of measurement, while larval wet weight shows no increase with time. Larval length tends to increase for 1–3 days after terminal yolk utilization and maximal embryo dry weight. Terminal yolk utilization may thus be the best indicator of time to first-feed larvae. These times can vary from 5–10 days posthatch, depending upon temperature-salinity conditions (Table 2). Striped bass larvae are quite resilient in that first-feeding can be delayed several days after terminal yolk utilization (Eldridge *et al.*, 1982); however, it is desirable to prevent the decreases in length and embryo weight occurring under these conditions.

The longest larvae were obtained at 14° C and 5 % salinity. Temperatures of 12° C are reportedly near the lethal levels (Hall, 1991). Doroshev (1970) reported 10° C to be lethal to larvae, with optimal survival at $15-19^{\circ}$ C. There is a possibility that progeny of a northern bass population might be more tolerant of low temperature than those of more southerly populations, but there seems little value, from a culture standpoint, in using lower temperatures than 14° C.

A salinity of 5 ‰ produced longer larvae than salinities of 1 or 10 ‰ for any given temperature – similar to the 7.9 ‰ reported by Doroshev to be optimal for survival. Hall (1991), in a review of available data, reported salinities of 0–15 ‰ suitable for larval survival. The estimated values of yolk and oil reserves present at hatch (72 and 80 μ g, respectively) are similar to the mean values reported by Eldridge *et al.* (1982), of 60 and 130 μ g, respectively, and within the range of values reported from several egg batches. Striped bass larvae hatched with 80 μ g of oil droplet. As found in earlier studies (Doroshev, 1980; Eldridge *et al.*, 1982), oil utilization was irregular

and nonlinear, so that linearly extrapolated times to terminal utilization were variable and usually much longer than times to terminal yolk utilization, averaging about a month for all treatments. Some of the irregularity in oil utilization was due to difficulty in measuring it gravimetrically. Image analysis of oil droplet size might yield better results.

CONCLUSIONS

- 1. We found a temperature-salinity combination of 14–16°C/5 ‰ to produce the longest striped bass larvae.
- 2. The assumption that the longest larvae should result in greater initial feeding success and hence better post-feeding survival requires further investigation.
- 3. The hypothesis that an increase in larval length correlates to greater locomotory capacity would be a logical future extension of this research, as would relating greater larval length to improved subsequent feeding and survival.

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