

Thermal preferenda and behavior of Atlantic eels (genus *Anguilla*) in relation to their spawning migration

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Synopsis

The final preferred temperatures (FPTs) of adult premigratory and migratory life-history phases of American eels, *Anguilla rostrata*, were determined by chronic tests in a horizontal thermal gradient. Mean FPTs were between 17 and 20°C and were not significantly different between life-history phases, acclimation temperatures, illumination regimes, photoperiods or sexual maturation states. Thermal behavior of eels was highly variable, both among individuals of the various test groups and among repeated tests of single individuals. Light inhibited behavioral thermoregulation by promoting shelter-seeking. The following inferences are drawn from the laboratory findings and observations of migrating *A. rostrata* and *A. anguilla* (European eels) in the North Atlantic: (1) decreasing temperatures may initiate downstream migration of silver eels, (2) eels may select temperatures close to their FPT in thermally stratified environments, but will tolerate higher and lower temperatures depending on illumination or other physical constraints, (3) the oceanic phase of the migration to the Sargasso Sea may take place at relatively shallow depths in the open ocean, probably within the upper 1000 meters. The strong eurythermality observed in eels may facilitate their occupation of and migration through thermally diverse and unpredictable habitats.

Introduction

The life history of freshwater eels of the Atlantic Ocean (genus *Anguilla*) involves a dramatic metamorphosis from a feeding and growth (yellow) phase in fresh or brackish water into a migratory (silver) phase. In late summer and fall, silver phase adults of both the American eel (*Anguilla rostrata*) and the European eel (*Anguilla anguilla*) move offshore towards the spawning area in the Sargasso Sea, located in the southwestern North Atlantic Ocean. Knowledge of the reproductive portion of eel life history is incomplete because it is based primarily on observations of adult, silver phase eels in the early stages of the migration (e.g. weir and

trap catches in rivers and estuaries, trawl catches and telemetric tracking studies) and on the distribution of newly hatched embryos in the southwestern Sargasso (McCleave 1987). Few observations of migrating adults have been made in waters overlying the continental shelf or the open ocean, and no adult eels have been observed in the spawning area (Tesch 1977).

Additional inferences about reproductive migrations have been drawn from laboratory studies involving the behavior, morphology and physiology of silver phase eels (Beatty 1975, Winn et al. 1975, Pankhurst & Lythgoe 1983, Kleckner 1980, Kleckner & Krueger 1981). Artificial maturation of silver eels produces further metamorphosis that is related

to adaptation to the oceanic environment, including increase in eye size, changes in skin pigmentation and structure, retinal organization, structure of skeletal muscle and degeneration of the intestine and olfactory epithelium (Boëtius & Boëtius 1967, Pankhurst 1982, Pankhurst & Lythgoe 1983, Sorensen & Pankhurst, 1988). Behavioral studies of artificially matured eels have provided insight on possible spawning mechanisms and behavior (Boëtius & Boëtius 1980, Sorensen & Winn 1984).

Temperature is a primary influence on the distribution of fishes. Laboratory estimates of thermal preferenda of many fishes generally correspond to temperatures occupied in the field (Coutant 1977, Magnuson et al. 1979). In this respect, it can be hypothesized that migratory *Anguilla* will be found at times, locations and depths that correspond to their final preferred temperature (FPT). Because freshwater, coastal and oceanic environments are temporally and spatially diverse with respect to temperature, eels should migrate through thermal environments at times and at depths corresponding to temperatures that maximize migratory and reproductive success.

Early juvenile *Anguilla* (glass eel phase) entering fresh water select temperatures of 20 to 25° C in still water, but select lower temperatures (to 6° C) in flowing water (Tongiorgi et al. 1986). Yellow phase *A. anguilla* generally increase activity with increasing ambient temperatures (Nyman 1972, Vøllestad 1986), while *A. rostrata* cease feeding, show reduced activity and become torpid (metabolically depressed) at temperatures below 10° C (Walsh et al. 1983). Barila & Stauffer (1980) found the final preferred temperature of *A. rostrata* in freshwater to be 16.7° C. Reanalysis of Barila & Stauffer's data by a more precise nonlinear method (Karlsson et al. 1984) yielded a different preference estimate of 17.4° C. However, no study to date has addressed specifically the long-term thermal preferenda of eels in the silver, migratory phase.

This study investigated the FPTs and thermal behavior of premigratory and migratory American eels in the laboratory and in nature. The objectives of the laboratory experiments were: (1) to determine the FPT of (a) premigratory freshwater yellow

low eels, (b) migratory freshwater silver eels, (c) saltwater-acclimated silver eels, and (d) artificially matured silver eels; (2) to determine the effects of acclimation temperature and photoperiod on FPT; and (3) to compare the effects of photoperiod, life history phase and maturation state on relative activity.

Experimental conditions (temperature, light and salinity) were chosen to simulate the range of physical conditions available in nature to premigratory, migratory and sexually mature eels to assess whether there are changes in FPT and thermal behavior associated with migratory metamorphosis, adaptation to the marine environment and sexual maturation. The possible thermal influences on eel migration and spawning were inferred by relating the laboratory observations of the thermal behavior of adult eels with: (1) the distribution and behavior of silver eels observed, captured or tracked in freshwater and waters overlying the continental shelf and open ocean, and (2) the thermal structure and chronology of the North Atlantic Ocean and its adjacent fresh and brackish waters that are inhabited by eels.

Methods

Experimental rationale

Chronic tests of thermal preference were chosen to avoid several disadvantages of acute tests, including the need for several temperature acclimation groups and error associated with extrapolation of acute thermal preference data to infer FPT. Because of the long period of gravitation (> 24 h), estimates of FPT using chronic tests are assumed to be independent of acclimation temperature (Reynolds & Casterlin 1979a, Houston 1982). However, as a test of the chronic method used here, eels were subjected to several acclimation temperatures before they were introduced into the gradient to verify the assumption that acclimation temperature has no effect on FPT. A horizontal thermal gradient was used to determine FPT because it provided experimental eels with nearly instantaneous ac-

cess to all temperatures in the range. The horizontal gradient could be shifted to observe behavioral reactions of eels to a changing thermal regime. Ambient light within the gradient could be altered to assess the effect of light intensity and photoperiod on FPT and activity.

Four separate thermal preference experiments were performed to assess the effects of acclimation temperature, acclimation photoperiod and maturation treatments on FPT of yellow and silver phase eels:

Experiment 1. This experiment addressed the effect and interaction of acclimation temperature and photoperiod on FPT of yellow eels. Yellow eels were acclimated in freshwater to temperatures of 10 and 20°C and to photoperiods of LD 12:12 and 16:8. Gradient salinity was 0‰; gradient temperature range was 10 to 25°C. Eight yellow eels from this group also were subjected to gradient shifts of $\pm 5^\circ\text{C}$ (gradient temperature ranges 5 to 20°C or 15 to 30°C) after the initial 48 h test period to determine if eels positioned themselves in the gradient in response to temperature alone.

Experiment 2. This experiment estimated FPT of silver eels in freshwater. Silver eels were acclimated in freshwater to 18°C and to LD 12:12. Gradient salinity was 0‰; gradient temperature range was 10 to 25°C.

Experiment 3. This experiment investigated the effects and interaction of maturation state and photoperiod on FPT of artificial seawater-acclimated silver eels. Silver eels were acclimated to 34 to 36‰ seawater at 18°C and to LD 12:12 and 0:24 (continuous darkness). Half the eels were artificially matured and half were unmatured and served as controls. Gradient salinity was 34 to 36‰; gradient temperature range was 10 to 25°C.

Experiment 4. This experiment investigated the effect of maturation state and low acclimation temperature on FPT of seawater-acclimated silver eels. Silver eels were acclimated to 34 to 36‰ seawater at 5°C and to continuous darkness. Half were artificially matured and half were unmatured. Gradient salinity was 34 to 36‰; gradient temperature range was 5 to 20°C. One silver eel was also subjected to several gradient shifts of $\pm 5^\circ\text{C}$.

Eel collection, acclimation and maturation

Yellow eels between 300 and 450 mm total length (TL) were collected during June and July 1988 from Sedgeunkedunk Stream, Penobscot Co., Maine by electrofishing. Small (< 450 mm TL), presumably male, silver eels were obtained from commercial weirs on Sedgeunkedunk Stream and Mill Stream, Lincoln Co., Maine during the downstream migration in September and October 1988. Eels were transported to the laboratory on ice. They were held unfed in 1000 liter circular tanks in fresh water or 34 to 36‰ artificial sea water for at least 4 weeks prior to FPT experiments to allow for physiological temperature acclimation. Male silver eels to be artificially matured were given a single intramuscular injection of 500 IU of human chorionic gonadotropin (HCG; Sorensen & Winn 1984), marked by freeze branding (Sorensen et al. 1983) and held at 18°C. Sexual maturation was complete approximately 4 weeks after injection; eels developed black pigmentation on the fins, enlarged eyes, swollen abdomens and discharged sperm. Eels used in Experiment 4 were allowed to mature at 18°C before they were subjected to a 6 weeks acclimation period at 5°C. After testing, eels were sacrificed and the following characteristics were measured: total length (nearest 1 mm), eye length and height (nearest 0.1 mm), total weight (nearest 0.1 g), and gonad weight (nearest 0.01 g).

Experimental apparatus and technique

Eels were tested in a custom-designed horizontal gradient chamber that utilized a cross-gradient water flow to establish and maintain a uniform thermal gradient (Fig. 1). The chamber is a modified version of a behavioral trough used for olfactory preference experiments by Jones & Hara (1985). Water flow was perpendicular to the axis of the gradient; this eliminated bias due to rheotactic behavior induced by horizontal gradients that utilize along-axis flow to establish the gradient (McCauley 1977, Coutant et al. 1984).

Chamber lighting was provided by 4 40-watt

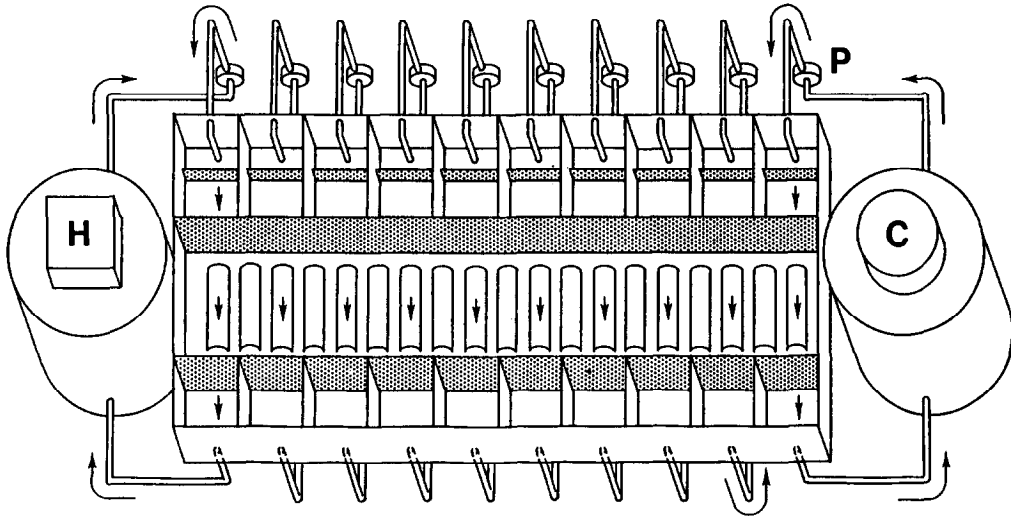


Fig. 1. Diagram of an overhead view of the thermal gradient tank (length = 2.44 m, width = 1.12 m, depth = 0.4 m, water depth = 5 cm). Stippled panels are perforated opaque plastic, tank walls and baffles are plexiglas. The central chamber occupied by the test eel measures 2.44 m by 0.5 m. The tank is divided into 10 'cells'; each cell possesses its own pump that recirculates water from the cell outflow to the cell inflow (return flow is directed underneath the tank and back to pump of the same cell). Temperature limits of the gradient are controlled by a heating reservoir connected to the return circuit of one end cell of the tank and a cooling reservoir connected to the return circuit of the other end cell. Cells are joined in the central chamber, allowing passive mixing of water and establishment of a continuous temperature gradient (arrows indicate direction of flow). Flow within the chamber is non-laminar and ranges from 1 to 2 cm · sec⁻¹. Vigorous aeration of water in the heating reservoir prevents oxygen supersaturation; dissolved oxygen measured in all portions of the gradient is at or near saturation. To reduce searching or escape behavior of eels in the gradient, 19 opaque plastic hiding tubes (7.6 cm dia., 30 cm long) cut in half longitudinally are attached to the bottom of the inner chamber. Thermistors (omitted) are located in alternate tubes. Tubing and heater/chiller reservoirs are thermally insulated. C = chiller, H = heater, P = pump.

white incandescent bulbs during the period of subjective day ($0.15 \mu\text{W} \cdot \text{cm}^{-2}$ at the water surface) and 4 25-watt red incandescent bulbs during the period of subjective night ($0.015 \mu\text{W} \cdot \text{cm}^{-2}$ at the water surface). The level of illumination during subjective day was above the threshold for synchronization of locomotor activity ($0.01 \mu\text{W} \cdot \text{cm}^{-2}$ for white light, van Veen & Andersson 1982). Because the visual pigments of eels have maximal absorbance in the blue and green portion of the spectrum (Beatty 1975), they are minimally sensitive to red light. Thus the low level of red illumination utilized during subjective night (necessary for video recording) was assumed to be perceived as relative darkness by an eel in the gradient. A timing circuit provided a 15-min dimming period between day and night illumination regimes.

Eels were tested singly in the gradient. At the start of the testing period, an eel was dip-netted from the acclimation tank and introduced into the

region of the gradient that corresponded to the acclimation temperature. The eel was then allowed to move freely in the chamber for the duration of the test.

Temperatures in the gradient were measured by 10 thermistors positioned in alternate tubes. A computer-controlled data acquisition system recorded temperatures in all 10 tubes at 10 min intervals. Temperatures in tubes without thermistors were interpolated with an algorithm (determined by previous calibration) that used temperatures measured in the two adjacent tubes. Measured and calculated tube temperatures were accurate to within 0.5°C .

Position and behavior of eels within the gradient was recorded by an overhead video camera and time-lapse videotape recorder with a time-date generator. Videotapes were viewed and stopped at each 10 min interval corresponding to the times when gradient temperatures were recorded. The

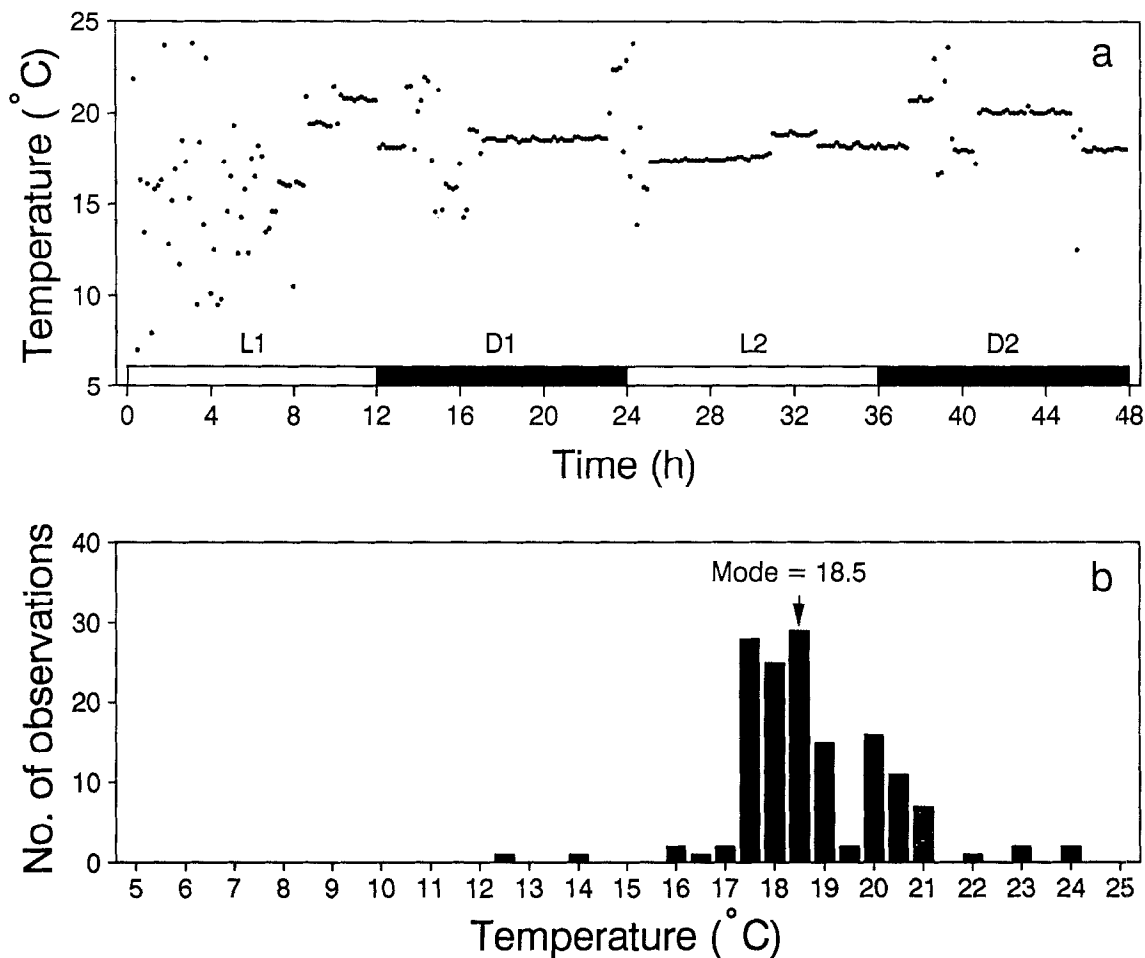


Fig. 2. a – Example of a typical temperature-time track for a yellow eel acclimated to 20°C, LD 12: 12 (Experiment 1). Data points are at 10 min intervals. Temperatures in the thermal gradient chamber ranged from 5 to 25°C. b – Distribution of occupied temperatures during LD2 (L2 + D2) of the same fish (total number of observations = 144; bin labels are midpoints of each bin, e.g. 18 = 17.75–18.25). The modal temperature of 18.5°C is the estimated FPT for this fish.

tube number (1 through 19) that the eel occupied at that time was recorded (eels could be followed from tube to tube during videotape playback and their location determined even when inside a tube and not directly visible). Rarely, when the eel was not in a tube at the 10 min interval, the number of the tube closest to the midpoint of the eel's body was recorded. Gradient temperature and eel position were then combined to determine the temperature occupied by the eel in the gradient every 10 min throughout the test period. Each occupied temperature estimate constituted one observation (144 observations per 24 h period).

Data analysis

Only observations during the second 24 h of testing [e.g. subjective day (L2), subjective night (D2) or both periods pooled (LD2)] were used to calculate FPT. Occupied temperature estimates were separated into 0.5°C bins, and the mode of the resulting distribution served as the measure of FPT (Fig. 2). The mode was chosen as the estimator of FPT because it represents the most frequently occupied temperature during the observation period and is less sensitive to extreme values than the mean or median (McCauley 1977). Each modal FPT esti-

mate was considered a single independent data point for subsequent analyses (Mathur & Silver 1980). Comparisons of mean FPT between treatments (eel phase, acclimation temperature, maturation state, photoperiod or illumination level) were made using t-tests or analyses of variance (ANOVA; Sokal & Rohlf 1981).

Activity of eels was measured by analyzing movements of eels from one tube to another as recorded by the videotape system. If an eel moved from one tube to another tube between observations, activity was scored as 1 for that 10 min interval; if the eel remained in the tube, activity was scored as 0. An index of relative activity (range 0 to 1) was constructed for each selected time interval (e.g. L2, D2) by averaging activity scores over the interval.

Results

Experiment 1 – yellow eels acclimated to 10 and 20° C freshwater

Mean LD2 FPT of yellow eels was 18.81° C for all treatments pooled (Table 1, Fig. 3). FPTs of yellow eels during L2 and D2 periods were not significantly different for any treatment (paired comparisons t-test, $p > 0.05$). Mean LD2 FPTs of yellow eels

were not significantly different between acclimation temperatures ($p = 0.935$) or photoperiods ($p = 0.978$), and there was no significant interaction of the two treatments ($p = 0.209$; 2-way ANOVA). Activity indices were significantly higher during D2 than during L2 for yellow eels acclimated to the 12 : 12 photoperiod ($p = 0.003$ and 0.048 for 10° C and 20° C acclimation temperatures, respectively) but were not significantly different for yellow eels acclimated to the 16 : 8 photoperiod ($p > 0.10$ for both acclimation temperatures; paired comparisons t-tests).

Experiment 2 – silver eels acclimated to 18° C freshwater

Mean LD2 FPT of silver eels in freshwater was 19.57° C (Table 1, Fig. 3). FPTs of freshwater silver eels during L2 and D2 periods were not significantly different ($p > 0.10$; paired comparisons t-test). Activity indices of freshwater silver eels were significantly higher during D2 than during L2 ($p = 0.015$; paired comparisons t-test).

Table 1. Summary of experimental conditions, final preferred temperatures and activity indices from the second 24 h period (LD2) for the 4 experiments (fw = freshwater, SEM = standard error of the mean).

Experiment	Eel phase	Acclimation			Maturation state	n	LD2 Final preferred temperature (° C)		Mean activity index	
		Salinity (‰)	Temperature (° C)	Photoperiod (L : D)			Mean	SEM	L2	D2
1	Yellow	0 (fw)	20	16 : 8	–	6	19.83	1.32	0.144	0.170
	Yellow	0 (fw)	20	12 : 12	–	6	17.91	1.69	0.201	0.267
	Yellow	0 (fw)	10	16 : 8	–	6	17.75	1.70	0.125	0.263
	Yellow	0 (fw)	10	12 : 12	–	6	19.75	1.27	0.090	0.407
2	Silver	0 (fw)	18	12 : 12	–	13	19.57	1.00	0.091	0.165
3	Silver	34–36	18	12 : 12	matured	6	18.08	1.03	0.036	0.110
	Silver	34–36	18	0 : 24	matured	6	17.50	1.24	0.062	0.170
	Silver	34–36	18	12 : 12	unmatured	6	18.91	1.67	0.087	0.175
	Silver	34–36	18	0 : 24	unmatured	6	15.75	1.87	0.069	0.078
4	Silver	34–36	5	0 : 24	matured	9	17.17	0.71	0.163	0.175
	Silver	34–36	5	0 : 24	unmatured	5	17.80	1.34	0.158	0.103

Experiment 3 – silver eels acclimated to 18° C saltwater

Mean LD2 FPT of silver eels acclimated to 18° C saltwater was 17.56° C for all treatments pooled (Table 1, Fig. 3). FPTs of saltwater silver eels during L2 and D2 periods were not significantly different for any treatment ($p > 0.10$; paired comparisons t-tests). Mean LD2 FPTs of saltwater silver eels were not significantly different between maturation states ($p = 0.761$) or photoperiods ($p = 0.222$), and there was no significant interaction of the two treatments ($p = 0.396$; 2-way ANOVA). Activity indices were significantly higher during D2 than during L2 for eels acclimated to the 12 : 12 photoperiod for both matured ($p = 0.021$) and unmatured ($p = 0.003$) treatments. Matured eels acclimated to continuous darkness had significantly lower activity during the third 12h dark period (subjective L2) than during the fourth 12h dark period (subjective D2) ($p = 0.004$), but there was no significant difference in activity between periods for unmatured eels acclimated to continuous darkness ($p > 0.10$; paired comparisons t-tests).

Experiment 4 – silver eels acclimated to 5° C saltwater

Mean LD2 FPT of silver eels acclimated to 5° C saltwater was 17.39° C for pooled matured and unmatured eels (Table 1, Fig. 3). FPTs of 5° C-acclimated silver eels during L2 and D2 periods were not significantly different for matured ($p > 0.10$) and unmatured ($p > 0.10$) groups (paired comparisons t-tests). Mean LD2 FPTs were not significantly different between maturation states ($p = 0.633$; t-test). There was no significant difference in activity between the third and fourth 12h dark periods (subjective L2 and D2) for matured and unmatured eels (pooled) acclimated to continuous darkness ($p > 0.10$; paired comparisons t-test).

Comparison of FPTs

Mean FPTs of groups of eels from the four experi-

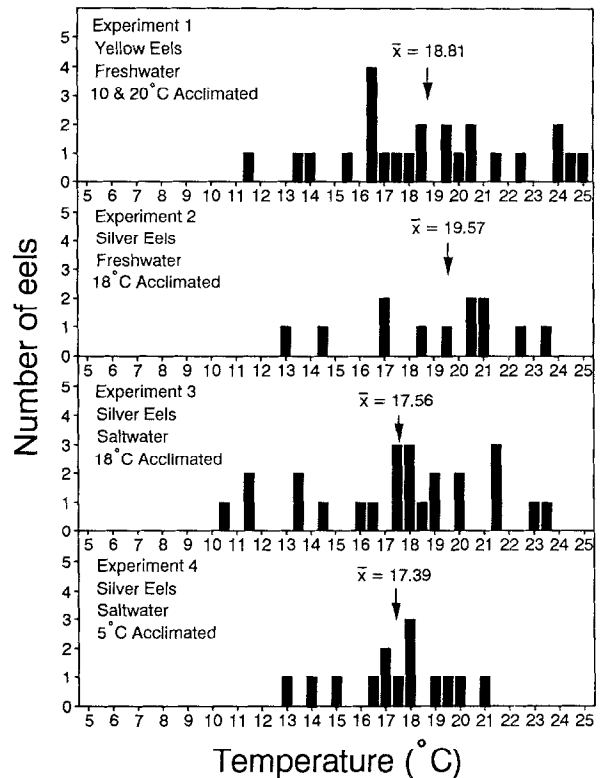


Fig. 3. Distributions of FPTs for eels in Experiments 1–4. Temperature limits of the thermal gradient were approximately 10–20° C for yellow eels, freshwater silver eels and 18° C acclimated saltwater silver eels, and approximately 5–20° C for 5° C acclimated silver eels.

ments were not significantly different ($p = 0.219$; one-way ANOVA), but FPTs of individual eels varied widely (range 10.5 to 25° C, Fig. 3). Because eels were held in acclimation tanks 7 to 202 d before testing, the effect of holding time on FPT was considered. There was no significant correlation between FPT and days post-collection for any of the four groups (range of r values = 0.074–0.286, $p > 0.20$ in all cases; significance tests for correlation coefficient). Similarly, gonosomatic index of matured eels was considered as a factor in affecting FPT, since it varied considerably (1.66 to 19.24% of total body weight). There was no significant correlation between FPT and gonosomatic index for matured silver eels acclimated to 18° C ($r = 0.370$, $p = 0.241$) or 5° C ($r = 0.641$, $p = 0.066$; significance tests for correlation coefficient).

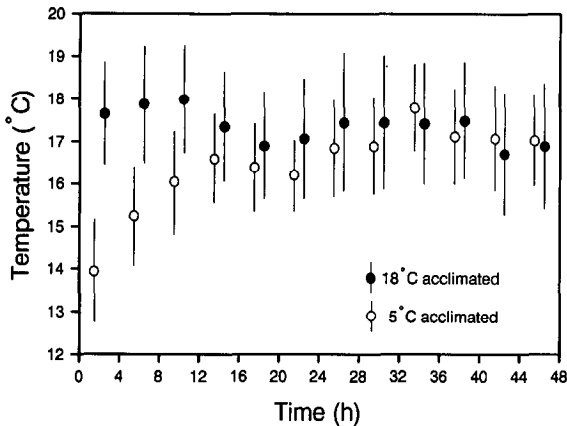


Fig. 4. Mean occupied temperatures of silver eels acclimated to 18°C saltwater (solid circles, Experiment 3, $n = 24$) and 5°C saltwater (open circles, Experiment 4, $n = 14$) and 95% confidence intervals (vertical lines). Means and confidence intervals are from observations pooled over 4 h intervals. Note convergence of means and confidence intervals after approximately 16 h.

Eel thermal behavior and response to gradient shifts

Behavior of eels during thermal preference testing usually consisted of high activity during the first 12 h, followed by reduced activity and gravitation towards the FPT (Fig. 2). Gravitation to the FPT was usually complete by the end of the first 24 h period (Fig. 4). However, some individuals displayed continued high activity throughout the test period (i.e. swimming along walls of the chamber), or continued low activity (i.e. remaining in single tubes or corners). During the 4 weeks temperature acclimation period both yellow and silver phase eels acclimated to 5 or 10°C temperatures showed reduced activity and response to physical stimulation.

Shifting the thermal gradient after an eel had selected a FPT usually resulted in movement of the eel to a new tube or area that contained temperatures at or near the FPT (Fig. 5). Yellow eels that experienced gradient shifts during light periods commonly did not move to a new tube until after the lights dimmed (Figs 5a, b). During these light periods, yellow eels tolerated temperatures as high as 30.5°C during shifts to warmer gradient ranges and as low as 8°C during shifts to colder gradient

ranges. The silver eel subjected to multiple gradient shifts under constant dim red light appeared to move freely from tube to tube during gradient shifts (Fig. 5c). Eels therefore appeared to position themselves in the gradient primarily in response to temperature, but their movement from tube to tube was inhibited during light periods.

Discussion

Thermal preference experiments

The mean FPT determined for yellow phase *A. rostrata* in this study (18.81°C; Experiment 1) is slightly higher than that determined by Karlsson et al.'s (1984) reanalysis of Barila & Stauffer's (1980) experimental data (17.4°C). The wide range of individual FPTs (maximum 13.5°C in yellow eels) found in this study is comparable to ranges of thermal preference within Barila & Stauffer's acute temperature acclimation groups. Because activities and behaviors of eels in the thermal gradient were variable, the differences in individual FPT may be due to the reaction of some eels to the experimental environment that inhibited their normal gravitation to the final preferendum (e.g. reluctance to leave a tube during light periods, stimulation of activity in a novel environment). Repeated 48 h tests of individual eels produced FPT ranges of 15.0 to 18.5°C and 19.5 to 22.5°C in two matured silver eels and 15.5 to 22.5°C in one unmatured silver eel. Because eel behavior in general is considered to be highly variable, wide variability in FPT is not a surprising result.

Eels did not express differences in thermal preference between light and dark periods, as has been found in some other fishes (Brett 1971, Reynolds & Casterlin 1979b), yet their activity may be inhibited during light periods. Varying photoperiod (LD 16 : 8, 12 : 12 and continuous darkness) also did not alter thermal preference of eels. Artificial maturation had no effect on FPT in silver eels. However, the ability to detect small differences of FPT in these experiments is reduced because of the small sample sizes and individual variability in eel behavior and FPT. There appears to be no significant

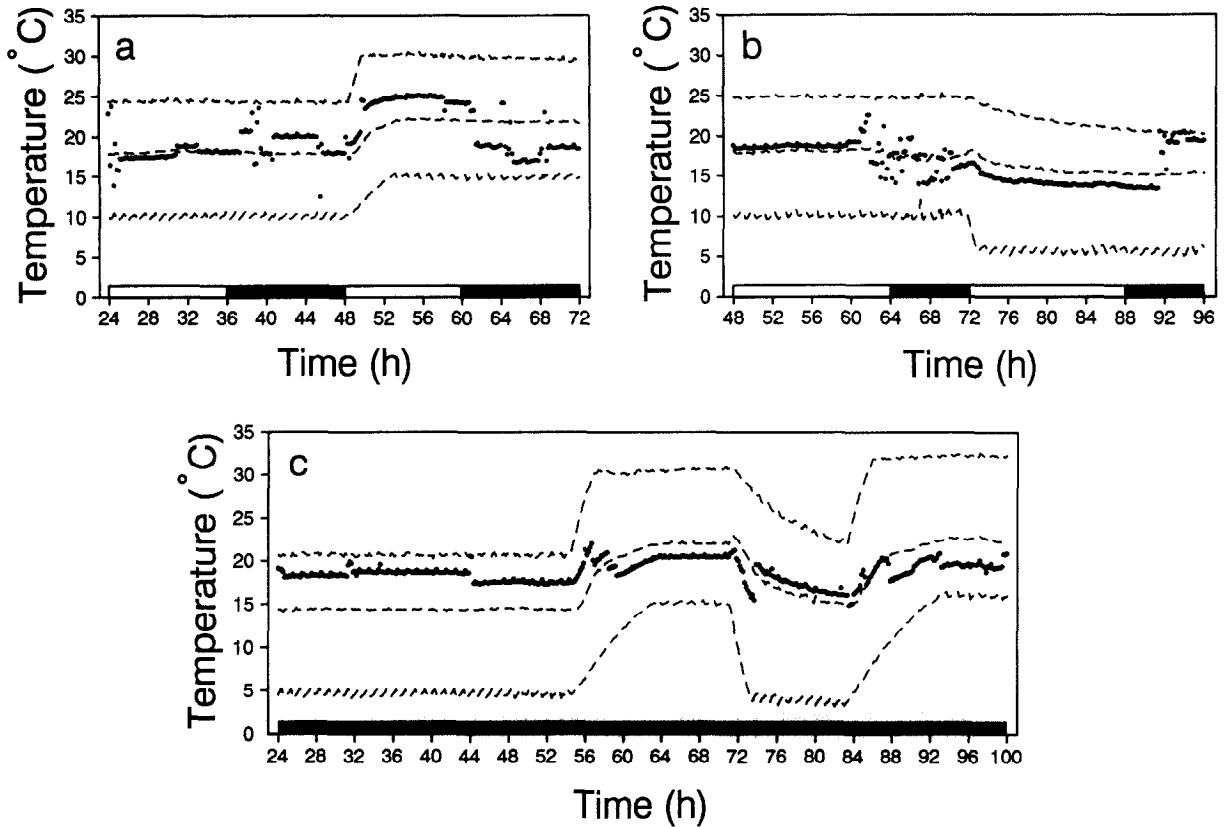


Fig. 5. Examples of gradient shift experiments (Experiments 1 and 4). Dashed lines are temperatures at the warm end, center, and cold end of the thermal gradient. Solid circles are temperatures occupied by the eel. a – Temperature-time track of yellow eel (acclimated to 20°C, LD 12:12) with gradient shift from 10–25°C to 15–30°C (first 24 h of data omitted). b – Temperature-time track of yellow eel (acclimated to 10°C, LD 16:8) with gradient shift from 10–25°C to 5–10°C (first 48 h of data omitted). Note reduced movement from tube to tube during light periods following gradient shift and return to original preferred temperature range after dark. c – Temperature-time track of matured silver phase eel (acclimated to 5°C and continuous darkness) with 3 gradient shifts (first 24 h of data omitted). Note uninhibited movement of the eel to tubes containing temperatures (15–22°C) at or near the LD2 FPT (19°C).

change in FPT in eels as they change from the nonmigratory yellow phase to the migratory silver phase, adapt to the marine environment, and become sexually mature.

Downstream migration

The FPT of silver eels in freshwater (19.57°C; Experiment 2) is considerably higher than Vøllestad et al. (1986) estimate of temperature of maximum downstream migration for *A. anguilla* (9°C) and range of water temperatures at the day of 5% cumulative silver eel descent (10.8 to 15.6°C). Therefore, downstream migration of silver eels appears

to occur at temperatures lower than the FPT. However, Vøllestad et al. noted that there was no exact threshold temperature that initiated downstream migration, and few eels were caught when temperatures were above 18°C or below 4°C. In Vøllestad et al. (1986) field experiments, temperature was highly correlated with the start of runs and with percent recapture of silver eels released upstream of the weir in which they were initially caught. Because temperatures below approximately 10°C appear to inhibit activity of silver eels, downstream migration may be triggered within a temperature window from about 10°C (lower limit of activity) to 18°C (the FPT). A rapid drop in temperature within this thermal window may serve as the actual

migratory trigger, yet other factors such as weather, lunar phase and flow may also initiate or modulate the timing and intensity of eel runs (Deelder 1954, Boëtius 1967, Vøllestad et al. 1986). Westin & Nyman (1975) noted that silver eels held in the laboratory increased their activity during periods of decreasing temperature and speculated that a drop in temperature stimulates downstream migration.

Coastal migration

Silver phase *A. rostrata* have been observed in coastal waters during months immediately following the peak of downstream migration (Table 2) at temperatures of 8 to 17°C. The mean preferred temperature of unmaturing silver eels acclimated to saltwater (17.3°C; Experiment 3) is slightly higher than this range. Tesch (1972) noted that *A. anguilla* tracked in water less than 6°C displayed no migratory activity and either drifted passively or remained stationary on the bottom.

Eels tracked in coastal waters occupy a variety of depths and change depth frequently (Stasko & Rommel 1977, Tesch 1979, Tesch 1989, Arnold & Cook 1984). General patterns of eel behavior in coastal environments indicate that under stratified conditions eels may occupy deeper waters during the day at temperatures below their preference but migrate to warmer surface water at night (Westerberg 1979, Tesch 1989). Eels tracked in the western Mediterranean Sea tended to swim in the 13°C hypolimnion, but regularly crossed the thermocline during vertical migrations (especially at night) into surface waters as warm as 18°C (Tesch 1989). Westerberg (1979) tracked one eel in a thermally stratified portion of the southern Baltic that swam at night at mid-depths where temperatures were between 12 and 14°C, but descended to the bottom during the day, where temperatures were approximately 6°C. In the central Baltic Sea, tracked eels preferred to swim above the thermocline both day and night, usually at temperatures above 10°C (Tesch et al. 1989).

Table 2. Locations, depths and corresponding water temperatures of silver phase American eels captured or observed in continental shelf waters.

Location	Number	Date	Latitude/longitude	Depth	Temperature (°C)		Reference
					Surface	Bottom	
East of Cape Cod	1	7 Nov	41° 40.5N 69° 39W	0–82 m	10.8	8.5	Wenner (1973)
East of Cape Cod	1	7 Nov	41° 38N 69° 42W	0–55 m	10.8	9.0	Wenner (1973)
Rhode Island	–	–	off Block Island	–	–	–	Winn & Hammen (1969)
Southeast of Chesapeake Bay	1	5 Dec	35° 51N 75° 30W	0–18 m	10.7	10.7	Wenner (1973)
Southeast of Chesapeake Bay	1	5 Dec	35° 41N 75° 18W	0–22 m	11.3	11.4	Wenner (1973)
Southeast of Chesapeake Bay	1	5 Dec	35° 25N 75° 18W	0–24 m	12.0	12.0	Wenner (1973)
East of Assateague Island, Virginia	6	22 Dec	37° 51N 75° 19N	0–9 m	8	8	Wenner (1973)
Virginia	6	Nov	36° 15N 74° 13W	surface	16–17	–	F.G. Carey personal communication
North Carolina	–	–	8–16 km off coast	surface	–	–	Winn & Hammen (1969)
Georgia	several	Dec & Jan	3.2 km offshore of Altamaha River	0–15 m	–	–	Facey & Helfman (1985)
Florida	1	Nov	–	surface	–	–	Winn & Hammen (1969)

Oceanic migration

Observations of migrating eels in the open ocean (bottom depths > 200 m) are rare. Silver phase *A. anguilla* have been caught in the eastern North Atlantic by pelagic trawls towed at maximum depths of 325 m (Ernst 1975) and 500 m (Bast & Klinkhardt 1988). Silver eels have also been recovered from stomachs of bottom-dwelling fishes captured from a depth of more than 700 m (Reinsch 1968). One (possibly two) eels morphologically similar to silver phase *Anguilla* were photographed swimming on the bottom of the Tongue of the Ocean (Bahamas) by a submersible at a depth of 2000 m (Robins et al. 1979). Temperature at this depth was approximately 4°C (C.R. Robins personal communication). McCleave & Kleckner (1985) have proposed that migration in the open ocean occurs in the meso- or epi-pelagic zones, based on behavior of tracked eels and indirect evidence from morphological and physiological adaptations of eels to these environments.

Silver eels tracked as they left the continental slope off the Bay of Biscay and west of Spain occupied depths of at least 400 m but selected shallower depths (50 to 250 m) at night (Tesch 1978). As with Mediterranean eels, most of these fish swam in the hypolimnion (temperatures approximately 11 to 12°C) most of the time, but often crossed the thermocline into warmer water (12 to 15°C) at night.

Matured and unmatured *A. rostrata* in saltwater have mean FPTs of 17.5°C (Experiments 3 and 4) and may avoid temperatures greater or less than 5°C from their individual FPT based on gradient shift experiments. However, silver eels show strong photonegative behavior that may override thermoregulatory behavior under natural conditions. Tesch (1978) noted that vertical migration of eels tracked in the open ocean was strongly influenced by photic conditions (perhaps even by moonlight) and concluded that silver eels may be more sensitive to light than to temperature during oceanic migration. Migration in the open ocean thus may be similar to migration in stratified coastal environments, with eels occupying shallow, warm depths at night and diving to deeper, colder depths during the day to avoid high light intensities. From

behavioral and physiological evidence, eels should occupy only depths where temperatures exceed approximately 10°C. If so, eels would travel no deeper than about 1000 m in the open ocean, the approximate depth of the 10°C isotherm in the open North Atlantic north of the spawning area (Fuglister 1960). However, the putative observation of *Anguilla* in 4°C water at 2000 m in the Tongue of the Ocean suggests the thermal and depth limits may be much lower and deeper.

Depth of spawning

Castonguay & McCleave (1987) found that *Anguilla* embryos < 5 mm long were distributed in the spawning area at depths between 50 and 300 m and postulated that this represented the range of depth of adult spawning. Temperatures at these depths are 18 to 24°C; near or above the mean FPT of sexually mature *A. rostrata* (17.5°C; Experiment 4). Thus, spawning may occur at depths near the FPT.

Selection of appropriate temperatures also may be important in the timing of sexual maturation preceding spawning. Full sexual maturation in male *A. anguilla* takes about 20 d at 25°C and about 60 d at 15°C, but gonadal development may not progress at temperatures below 10°C (Boëtius & Boëtius 1967). Therefore, selection of temperatures below the FPT during migration may result in delayed gonadal maturation and conservation of energetic stores. Upon arrival at the spawning area, eels have access to warm surface layers that accelerate maturation in preparation for spawning. Fontaine et al. (1985) noted increased gonosomatic indices and pituitary gonadotropic function in female *A. anguilla* held in cages at 450 m depth compared to laboratory-held controls, suggesting that increased pressure (albeit at comparatively shallow depths < 500 m) may also be a factor in sexual maturation of eels.

Summary and conclusions

The temperatures occupied by *Anguilla* in nature

are often quite different from estimates of their thermal preferences. Migratory eels may be found in waters of temperatures from 4 to 20° C and do not appear to occupy any single specific temperature during migration. Thus, the hypothesis that preferred temperature strictly dictates the timing of movements and distribution of migratory eels cannot be confirmed.

However, several trends in the thermal behavior of eels are evident. First, downstream migration appears to be initiated as temperatures drop below the range of FPTs (17 to 20° C). The exact nature of the thermal cue (threshold temperature or rate of temperature decrease) and its importance in relation to other migratory cues remain unresolved. Second, migratory activity continues at temperatures equal to, but more often below, the preferred temperature range. In unstratified waters this can be due to local conditions where eels cannot make thermal choices, but in stratified waters other factors (especially light) may force eels into deeper, colder waters. Third, migratory activity may be inhibited at temperatures below approximately 10° C.

Whether temperature is used as an orientation cue in migration to the spawning area remains unresolved. Eels probably do not use temperature as an orientation mechanism in the manner proposed by Westin & Nyman (1975) who hypothesized that migrating eels actively avoid colder water and thus arrive at the warmest area of the North Atlantic, the Sargasso Sea. The horizontal scale of the thermal gradient of the North Atlantic is probably much too large to be detected by eels and used as an axis of orientation. Also, the coastal and oceanic environments are highly heterogeneous with respect to temperature and thus present many opportunities for migratory error to an eel guided by thermal gradients alone. However, because eels respond behaviorally to temperature gradient shifts of at least 5° C in the laboratory, they should be able to perceive relatively small differences in water temperature on a local scale that would allow them to identify strong thermal gradients, such as

the thermocline or frontal regions separating water masses of differing temperature.

The thermal behavior of *Anguilla* parallels other life history traits that characterize eels as ecological generalists that are tolerant of a wide range of environmental conditions. Because they are distributed over an enormous geographic range as larvae, adults must migrate back to the Sargasso Sea under a variety of thermal conditions that are dictated by latitude, hydrography and distance to the spawning area. Therefore, eels employ a high degree of thermal tolerance in order to successfully migrate through these variable and often unpredictable thermal environments and arrive at a warm subtropical pelagic water mass where currents maximize dispersal of larvae to appropriate habitats (Helfman et al. 1987). *Anguilla* may thus be considered a genus of subtropical oceanic origin that has adapted to thermally diverse environments during the growth phase and the spawning migration.

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