

Abstract—Spontaneous behavior of young red drum *Sciaenops ocellatus* was examined over a period of 8 h at two acclimation temperatures (21° and 26° C) and after acute temperature changes between these levels. Three sizes of fish were used (\bar{x} =9, 23, and 34 mmTL). Activity of fish acclimated to 26° C was greater than that at 21° C for fish of all sizes. Duration of pauses in spontaneous activity was generally lower at the warmer temperature. Effects of handling stabilized after 2–5 h. The time course for activity after an acute thermal change followed the traditional model for thermal stress, with an early overshoot followed by a stabilized period. The overshoot was positive for upward transfers (21–26° C) and negative for downward transfers (26–21° C). Pause duration showed a time course roughly inverse of the trend for activity, but pause frequency was inconsistent. Effects of 5° C changes stabilized after about 2 h. Results indicate that a minimum adjustment period of 2–5 h is advisable when handling young red drum for research or for stocking into natural waters. The behavior of young red drum deprived of food at acclimation temperatures suggests they are sweep, rather than saltatory, searchers.

Temperature effects on spontaneous behavior of larval and juvenile red drum *Sciaenops ocellatus*, and implications for foraging*

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Searching for food is critical to survival, and any factor that influences foraging behavior may have vital consequences, especially early in life when starvation is a serious threat. Temperature is one of the most potent natural factors affecting fishes, and substantial thermal variability may be experienced routinely. Such variability can span a wide range of time scales. Annual and seasonal differences in water temperature are common. Measurements of thermal effects on this scale probably reflect differences between physiologically stable (acclimated) states with respect to temperature. Differences in swimming performance due to acclimation temperature are well documented (Beamish 1978). Shorter-term temperature variations are also common in nature (summarized by Montgomery & MacDonald 1990). Fishes residing in shallow, lentic waters can experience large amplitude, diel temperature cycles (Bamforth 1962, Smid & Priban 1978). Movement across a thermocline imposes an even more rapid temperature change, as does inundation of tidal marshes and pools and the act of stocking hatchery fish into surface waters. Under these circumstances,

the dynamic processes of physiological adaptation to the temperature change also contribute to the overall thermal effect.

Our goal was to examine the effects of temperature on spontaneous behavior of young red drum *Sciaenops ocellatus*. Here, we construe spontaneous behavior of solitary young fishes deprived of food as that typically used in foraging. We designed experiments to evaluate differences in behavior at two constant temperatures and after acute increase or decrease in temperature. Our measures of behavior are useful for quantifying foraging effort.

Materials and methods

All fish were reared from eggs spawned at the Fisheries and Mariculture Laboratory of the University of Texas Marine Science Institute. Spawning occurred in the evening at 27–28° C. Eggs were collected the following morning and placed in 150 L rearing tanks maintained at two nominal acclimation temperatures (21° and 26° C), where they hatched within 24 h of spawning. Larvae were fed rotifers (*Brachionus*) at 3–4 d after hatching (3 mmTL); *Artemia* nauplii were added to the diet at 10–11 d after hatching. Roti-

fers were discontinued by day 15, when larvae were approximately 4–6 mm long. Dry food supplements were provided for larger fish, and *Artemia* densities were diminished so that juveniles eventually subsisted entirely on dry food. These and other details of rearing followed Holt et al. (1990).

Experimental design and protocol

Three sizes of red drum were studied. Mean (\pm SD) total lengths for the small, medium, and large size-classes were 8.7 (\pm 0.9), 22.8 (\pm 2.3), and 34.0 (\pm 2.6) mm. The lower acclimation temperature (21°C) is well below optimum for red drum larvae (Holt et al. 1981), so those reared at that temperature grew more slowly and exhibited higher mortality rates during the first week than did the 26°C fish. Trials were conducted at both nominal temperatures, yielding four treatments. Trials on fish placed in water of the same temperature as their rearing tank (acclimation temperature) are termed 'high' (26°C) or 'low' (21°C) controls. Trials at a temperature differing from the acclimation temperature are referred to as 'upward' (21° to 26°C) or 'downward' (26° to 21°C) transfers.

For each trial, fish were transferred individually from the rearing tank to separate transparent experimental arenas and left undisturbed for the duration of the observations. Arenas were rectangular from above, with sides in a ratio of 5:3. Arena sizes were scaled such that the longer dimension of the rectangular surface area was 6 to 8 times the average total length of the fish. Water depth was 4.6 to 7.5 times the greatest body depth of the fish (3.5 to 7.5 times depth with fins expanded). Small fish were pipetted individually, while larger fish were released from 100 mL beakers containing a single fish in 50 mL of water from the rearing tank.

Behavior was recorded on videotape through a camera mounted above the arenas. The recorder was activated from about 1 min prior to transfer until 20 min after transfer, then for 5-min periods at intervals increasing from 15 to 60 min. In all, behavior was quantified during 19 5-min observation periods beginning 5, 10, 15, 30, 45, 60, 75, 90, 105, 120, 135, 165, 195, 225, 255, 315, 375, 435, and 495 min after transfer. Each of the four treatments was applied to six fish.

Temperatures in rearing tanks were controlled by balancing air temperature with submersed aquarium heaters, and were slightly above nominal levels. Mean acclimation temperatures during the 10 d preceding each trial were 21.3–21.7°C and 26.1–26.5°C. Temperature in the experimental arenas was maintained by controlling room air temperature. This sufficed for trials with medium and large fish; however, arenas for small fish were placed in a larger water bath to stabi-

lize their temperature. During the 8h trials, the arena temperatures were 20.7–21.5°C and 26.1–26.5°C. By design, control fish were to experience no temperature change, and upward and downward transfers were to experience \pm 5.0°C. Actual differences between rearing tank and trial temperatures were -0.8° to $+0.2^\circ$ C for controls, $+4.5^\circ$ to $+5.0^\circ$ C for upward transfers, and -4.7° to -5.7° C for downward transfers.

In quantifying behaviors relevant to foraging, we recognized the dichotomy of searching techniques in fishes that travel in search of food and locate prey visually. Some species actively search while swimming and are called 'sweep' searchers (Laing 1938, O'Brien et al. 1986). Others search during brief periods when swimming is interrupted (described by Janssen 1982, and termed 'saltatory' searchers by O'Brien et al. 1989). Both types of active, visual foraging have been suggested for young fishes. For example, larval Atlantic herring *Clupea harengus* are thought to be sweep searchers (Rosenthal 1969, Rosenthal & Hempel 1970), while larval white crappie *Pomoxis annularis* exhibit saltatory searching behavior (Browman & O'Brien 1992). Bell (1990) suggested that the saltatory style is more generally employed by teleosts.

We examined three measures of foraging behavior: activity, pause frequency, and mean pause duration. Activity, the total amount of time spent swimming during each 5-min period, is a measure of foraging effort for sweep searchers, since they search new territory while swimming. Saltatory searchers use periods of inactivity (pauses) for finding food. Therefore, the frequency of pauses and their duration per observation period are indices of the time spent scanning the environment.

A BASIC computer program (available from the senior author) was written to act as an event recorder. Data were obtained by replaying the video tapes at normal speed and making the appropriate keystroke each time the subject's behavior changed (swimming, pausing). The program recorded intervals between keystrokes from which all variables were calculated. All observations from every trial (19 time-periods \times 6 replicates \times 4 treatments \times 3 sizes = 1368 5-min observation periods) were made by the junior author. When a selection of observation periods was reanalyzed, the differences in activity averaged 4.1% (extremes 0.1–9.2%) of the combined mean.

Data analysis

Since observations within each temperature treatment and size-class followed the same individuals over time, repeated-measures multivariate analysis of variance (MANOVA) was used to identify effects on spontaneous behavior due to fish size, temperature, and time

since transfer. Each behavioral measure (activity, pause frequency, pause duration) was considered the 'trials' factor in a separate analysis. Size-class and temperature treatment were grouping factors. Activity was restricted, by definition, to values between 0 and 300 s. Data were expressed as a percentage of the total time-period, and an angular (arcsine) transformation was applied to satisfy the statistical requirement of MANOVA for normality (Snedecor & Cochran 1967). Pause frequency and duration were not transformed.

Further analyses focused on three questions: (1) How does behavior differ at the two acclimation temperatures? (2) What is the immediate effect of a transfer of 5°C on behavior (relative to fish maintained at acclimation temperatures)? and (3) When does behavior stabilize after such a transfer? These questions were addressed by repeated-measures MANOVA on pairs of treatments within size-classes. Since temporal trends in variables were of greater interest than the mere presence of significant differences among the time-periods, we examined first (linear)- through fourth (quartic)-order polynomial trends over time with univariate *F* statistics (Wilkinson 1990), in addition to testing for significant differences due to temperature treatments within each time-period.

By design, fish transferred upward or downward experienced a temperature change, but control fish did not. However, behavior of all fish could be expected to vary with time, due to effects of handling, hunger, or circadian rhythms. Effects of handling should diminish with time since transfer, but hunger should increase over time and have a stronger influence on behavior of smaller fish. Therefore, behavior of fish in transfers was compared with that of control fish from the same acclimation temperature to answer questions (2) and (3). Specifically, upward transfers were compared with the low controls, and downward transfers with the high controls, to examine changes in behavior relative to acclimation levels. Figures 2, 4, and 6 depict the effects of thermal transfers as differences between means of six fish in the transfer and control treatments, but statistical tests were based on results for individual fish.

Results

Spontaneous behavior was composed of conspicuous periods of swimming activity interspersed with pauses, which were sometimes quite long. Behavior of medium and large fish was grossly similar, their transitions from active swimming to pausing were gradual, in part because of passive coasting. At the larger sizes, swimming involved forward movements generated by the caudal and pectoral fins and complex maneuvers us-

ing sculling motions of the pectoral fins alone. Movements of small fish were less fluid. Their small size and low velocities prevented them from appreciable coasting, so their motion stopped abruptly when propulsive strokes of the caudal region ceased.

Activity

The proportion of time in active swimming was high for all sizes, usually $\geq 65\%$. However, there were significant differences in activity among the three size-classes, among the four temperature treatments, and within individuals over the course of the experiments. When the four temperature treatments were examined separately, significant differences among size-classes were found only for downward transfers and high controls (Table 1).

Activity varied significantly with time during experiments within most temperature treatments for small and medium fish (Table 1). Large fish showed no significant changes in activity with time in any of the treatments because variability among individuals was greater than at smaller sizes. Differences in activity over time constituted temporal trends for small fish in all treatments and medium fish in downward transfers. These trends were usually linear, but several higher-order polynomials were significant for downward transfers (Table 1). In subsequent comparisons of the different temperature treatments, we examined each size-class separately because of the highly significant differences among sizes.

Controls Activity was generally greater at 26°C for all sizes of fish (Fig. 1). This difference was significant for small and medium fish, but the attained significance, *P*, for large fish was slightly beyond the criterion of $\alpha=0.05$ (Table 1).

Mean activity followed a monotonic trend with time at both temperatures for all sizes (Fig. 1). Small fish were most active immediately after transfer, while medium fish were least active at that time. Activity levels generally became stable within approximately 4 h. Mean differences (\pm SD) between the two control levels after 4 h were 40.0 (± 12.9), 49.1 (± 26.6), and 45.7 (± 41.5) s of swimming/5 min for small, medium, and large fish, respectively. Thus, there was remarkable similarity in the effect of acclimation temperature on mean activity, but variability increased steadily with size.

Significant differences between acclimation temperatures were common during the first 2 h of the trials, and rare thereafter (Fig. 1), suggesting that the effect of handling on activity and the rate of recovery were temperature-related. However, these effects of temperature were not consistent. Activity of small fish stabi-

Table 1

Significance levels (*P*) for *F* tests in repeated-measures MANOVA of activity in red drum *Sciaenops ocellatus*. Boldface values indicate effects significant at $\alpha=0.05$. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic, 3=cubic, 4=quartic).

Treatment	Effect	Size-class			
		All	Small	Medium	Large
All	Size	<0.001			
	Treatment	0.001			
	Time	0.001			
Upward transfer	Size	0.060			
	Time	0.477	<0.001 ¹	0.045	0.263
Low control	Size	0.092			
	Time	0.027	0.211 ¹	0.008	0.310
Downward transfer	Size	0.027			
	Time	<0.001	0.030 ^{2,3,4}	<0.001 ¹	0.856
High control	Size	0.037			
	Time	0.061	<0.001 ¹	0.168	0.193
High control vs. low control	Treatment		<0.001	0.035	0.058
	Time		<0.001	0.001	0.256
Upward transfer vs. low control	Treatment		0.031	0.536	0.554
	Time		<0.001	<0.001	0.807
Downward transfer vs. high control	Treatment		0.016	0.043	0.214
	Time		0.001	<0.001	0.974

lized sooner at low temperatures, but activity of medium fish stabilized later at low temperatures.

Transfers The general response to a 5°C change was an almost immediate shift in activity in the expected direction (upward transfers produced higher activity, downward transfers produced lower activity) to a level greater than the stabilized value attained after about 2.5 h (Fig. 2). In upward transfers, elevated activity persisted for 1–2 h, rising during the first 20–30 min from an implicit value of zero just prior to transfer. The response of fish to downward transfer was an almost immediate drop in activity to minimum values followed quickly by increasing activity (Fig. 2).

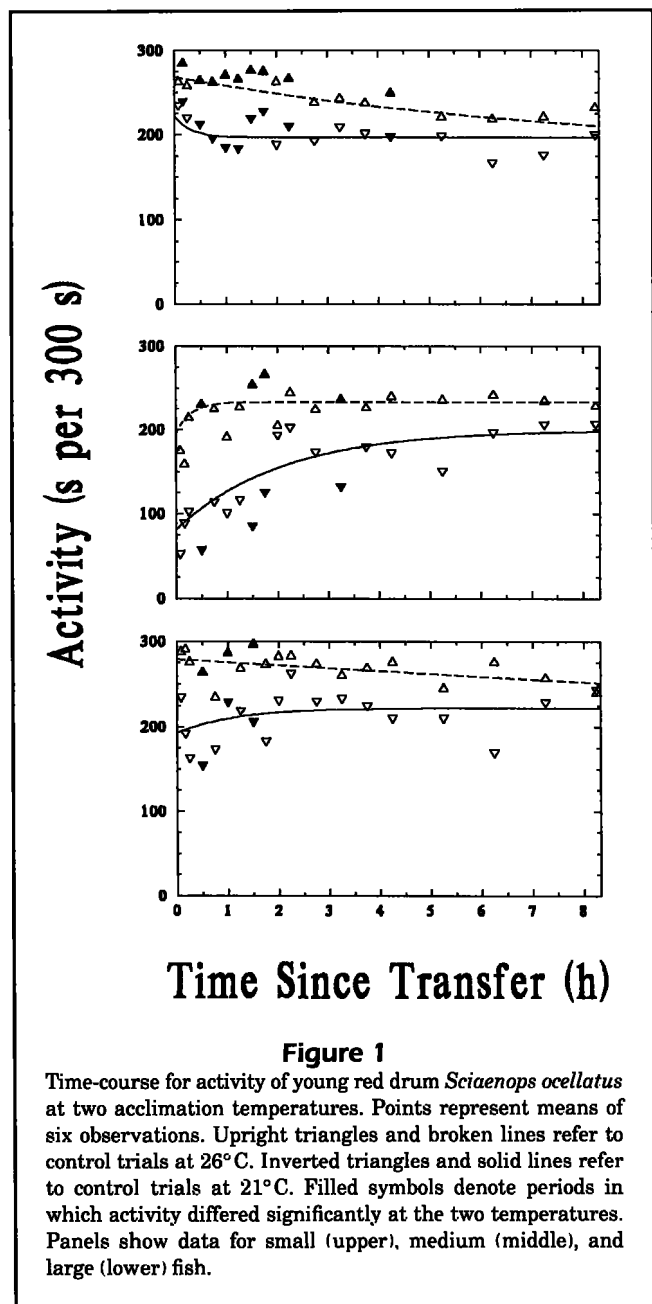
Activity of small fish after upward transfer was significantly different from that of low controls (Table 1). Differences were concentrated in the early part of the experiments, when transferred fish were more active than controls in six of the first seven time-periods (Fig. 2). Medium and large fish did not show overall differences between upward transfers and controls

(Table 1), and there were few significant differences at individual time-periods.

Downward transfer also had a significant influence on activity in comparisons with high controls, but only for small and medium fish (Table 1). Transferred fish were less active than controls in the first six time-periods for small fish and in five of the first nine time-periods for medium fish (Fig. 2). Large fish did not show an overall difference between downward transfer and control treatments, and only a single difference for individual time-periods was statistically significant (Fig. 2).

Pause frequency

The number of pauses during the 5-min observation periods generally decreased as fish grew (Fig. 3). Small control fish (temperatures and times combined) paused an average of 24.6 (± 11.5) times in 5 min; medium and large fish paused 10.8 (± 6.9) and 9.5 (± 7.3) times, respectively. All main effects (size-class, temperature



treatment, and time since transfer) had a significant influence on pause frequency. Differences among the size-classes were present within each of the treatments (Table 2).

Within individual fish (all sizes combined) there were significant differences in pause frequency with time in all treatments except the downward transfers (Table 2). These differences among time-periods followed linear trends in most temperature treatments for small fish. Among medium and large fish, temporal trends were less common, but curvilinear (quadratic) rela-

tionships were significant in two combinations of temperature treatment and size-class (Table 2).

Controls Pause frequency differed significantly between the two control temperatures for small and large fish (Table 2). For those sizes, pause frequency was higher at 21°C (Fig. 3).

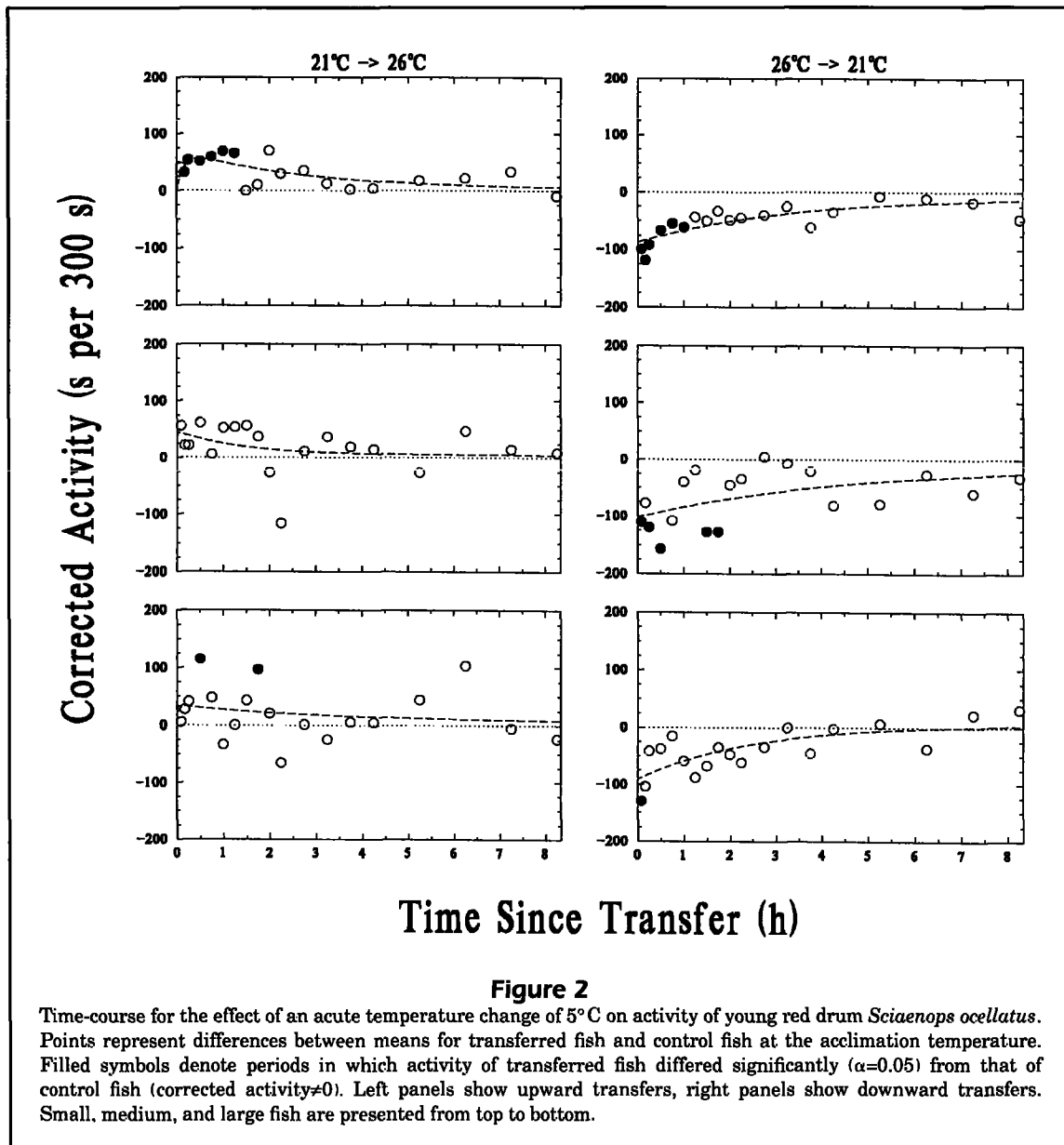
Pause frequency generally increased with time since transfer, but the amount of change during the experiment was small for medium and large fish. Temporal trends stabilized after about 2.5 h in most treatments (Fig. 3). Trends for small fish were parallel, with a mean difference of 13.6 (± 4.1) additional pauses/5 min at 21°C. Large fish had roughly parallel trends during the first 3 h, with a mean difference over that period of 7.5 (± 3.0) pauses. Mean differences between control values after behavior stabilized (3 h) were -12.9 (± 2.0), 0.2 (± 2.6), and -4.0 (± 2.4) pauses/5 min for small, medium, and large fish, respectively.

Differences between the control temperatures during individual time-periods were present throughout the experiments on small fish. For the two larger sizes, significant differences were confined to the first 2.5 h, highlighting the converging trends for those sizes. It appears that an immediate effect of handling is to depress pause frequency. The magnitude and duration of the effect is temperature-dependent.

Transfers Small and large fish showed qualitatively similar responses to the 5°C temperature change, relative to control values. Pause frequency was depressed by upward transfer. For the same size-classes in downward transfers, pause frequency increased slightly at first, then dropped to values below controls (Fig. 4). The response of medium fish to upward transfer was similar in form to the downward transfer of the other size-classes. In downward transfers their response was the same as that of low controls, producing a corrected pause frequency of zero. Variability in these apparent differences was great, and the only significant difference between transferred fish and their controls was for small fish in upward transfers (Table 2).

Small fish paused consistently and significantly less often after experiencing a 5°C increase (Fig. 4, Table 2). Large fish showed a similar, though smaller and non-significant, response. Mean differences between upward transfers and low controls were -6.8 (± 4.3) and -4.1 (± 2.8) s for small and large fish, respectively. Differences at individual time-periods were rare in upward transfers, at all sizes, but the overall effect of time since transfer was always significant (Table 2).

Downward transfer did not result in a significant overall effect on pause frequency, relative to controls, for small, medium, or large fish (Table 2). However, there were temporal trends in the differences between



downward transfers and high controls, centered near zero, that could not be detected by an overall test for a temperature effect. Corrected pause frequency of both small and large fish in downward transfers declined throughout the experiments, relative to high controls (Fig. 4). Time had a significant effect for these sizes but not for medium fish.

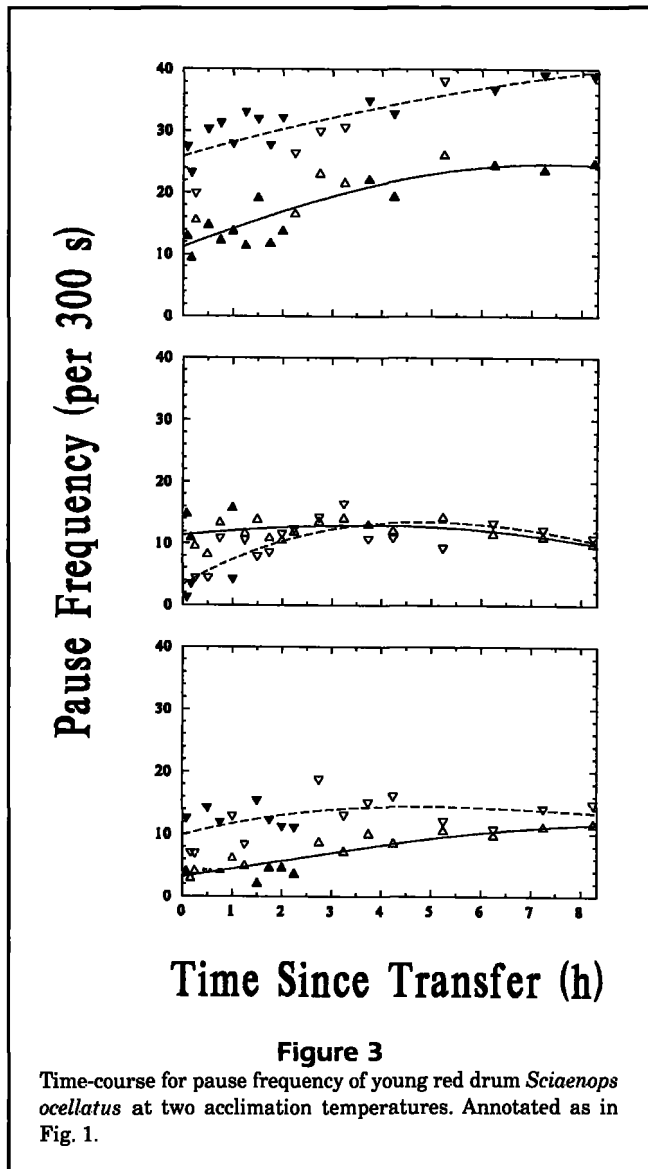
Pause duration

This variable showed the greatest range of variation, spanning more than two orders of magnitude (note varying scales in Figs. 5&6). Small fish showed little effect of time or temperature treatment on pause du-

ration, relative to effects on larger fish. At the two larger sizes, pauses were longest at the start of the experiments, stabilizing after about 2.5 h. As with the other behavioral measures, all main effects were significant (Table 3).

There were significant differences in pause duration among time-periods for low controls and downward transfers (Table 3). Linear, quadratic, and cubic trends described temporal changes for small and medium fish, but no trends were found for large fish.

Controls Pause duration was generally greater for fish maintained at 21°C than for those held at 26°C (Fig. 5). Largest differences occurred early in the ex-



periments and their magnitude varied greatly with fish size. Small fish showed the least difference between controls, with a maximum of 2.2 s. Mean values for medium fish controls differed by as much as 207.2 s during a given time-period (Fig. 5). Overall differences between the control temperatures were significant only for medium fish.

Pause duration was highest at the start of trials, with longer pauses at 21°C than at 26°C. Pause duration at the lower temperature decreased over time, approaching levels seen at 26°C, but remaining above them throughout the experiments (Fig. 5). This temporal trend was supported by a significant effect of time since transfer for medium fish, but a smaller change and greater variability precluded a

significant comparison for large fish (Table 3). Small fish showed much more subtle effects of transfer, although there was a significant effect of time due to a rising trend at 26°C. Pause duration generally decreased with time, reaching stable values within 1.5 h (Fig. 5). Mean differences (high control minus low control) after 2 h for small, medium, and large fish were $-0.2 (\pm 0.7)$, $-7.7 (\pm 3.9)$, and $-8.3 (\pm 19.2)$ s, respectively.

Transfers Upward and downward transfers had little effect on pause duration after about 2 h. The initial effect of a 5°C change on pause duration was consistent across the size-classes, but its magnitude varied greatly. Generally, an increase in temperature produced initially shorter pauses than in low controls. Downward transfer had the opposite effect, relative to high controls; pause duration increased. The medium size-class was affected most strongly (Fig. 6). The shock of an acute temperature drop was apparently more serious than a comparable increase in temperature. All size-classes showed a statistically significant change in pause duration after a drop in temperature, while none of the size-classes were significantly affected by an increase (Table 3). In contrast, temporal differences in pause duration were more prominent in upward transfers, where small and medium fish were significantly affected. Only medium fish showed significant differences with time in downward transfers, despite numerous significant differences at individual time-periods for small fish (Fig. 6).

Discussion

Transient thermal effects

The most widely accepted model for the time-course of adaptation of physiological rates to temperature change contains three phases (Kinne 1963, Prosser 1964, Precht et al. 1973). An initial shock reaction occurs during the first seconds to minutes, in which the rate overshoots the level expected for the new temperature. Over a period of minutes to hours, the rate returns from these extreme values to a stabilized level. The final stage occupies a prolonged period over which the final acclimated level is reached, but this may require weeks or months. This paradigm allows for two general cases. After exposure to a higher temperature, the overshoot for most measures is positive; the rate increases. When the destination temperature is lower than the acclimation temperature, the overshoot is negative (sometimes called an undershoot); the rate drops below that of the stabilized and acclimated levels for the colder temperature.

Table 2

Significance levels (*P*) for *F* tests in repeated-measures MANOVA of pause frequency in red drum *Sciaenops ocellatus*. Boldface values indicate effects significant at $\alpha=0.05$. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic).

Treatment	Effect	Size-class			
		All	Small	Medium	Large
All	Size	<0.001			
	Treatment	<0.001			
	Time	<0.001			
Upward transfer	Size	<0.001			
	Time	0.005	0.004 ¹	0.076 ²	0.122
Low control	Size	<0.001			
	Time	<0.001	0.023 ¹	<0.001 ¹	0.120
Downward transfer	Size	0.039			
	Time	0.544	0.010	0.114	0.944
High control	Size	0.001			
	Time	<0.001	0.001 ¹	0.778	<0.001 ^{1,2}
High control vs. low control	Treatment		<0.001	0.281	0.024
	Time		<0.001	0.003	0.001
Upward transfer vs. low control	Treatment		0.021	0.815	0.076
	Time		<0.001	<0.001	0.009
Downward transfer vs. high control	Treatment		0.979	0.945	0.489
	Time		<0.001	0.529	0.018

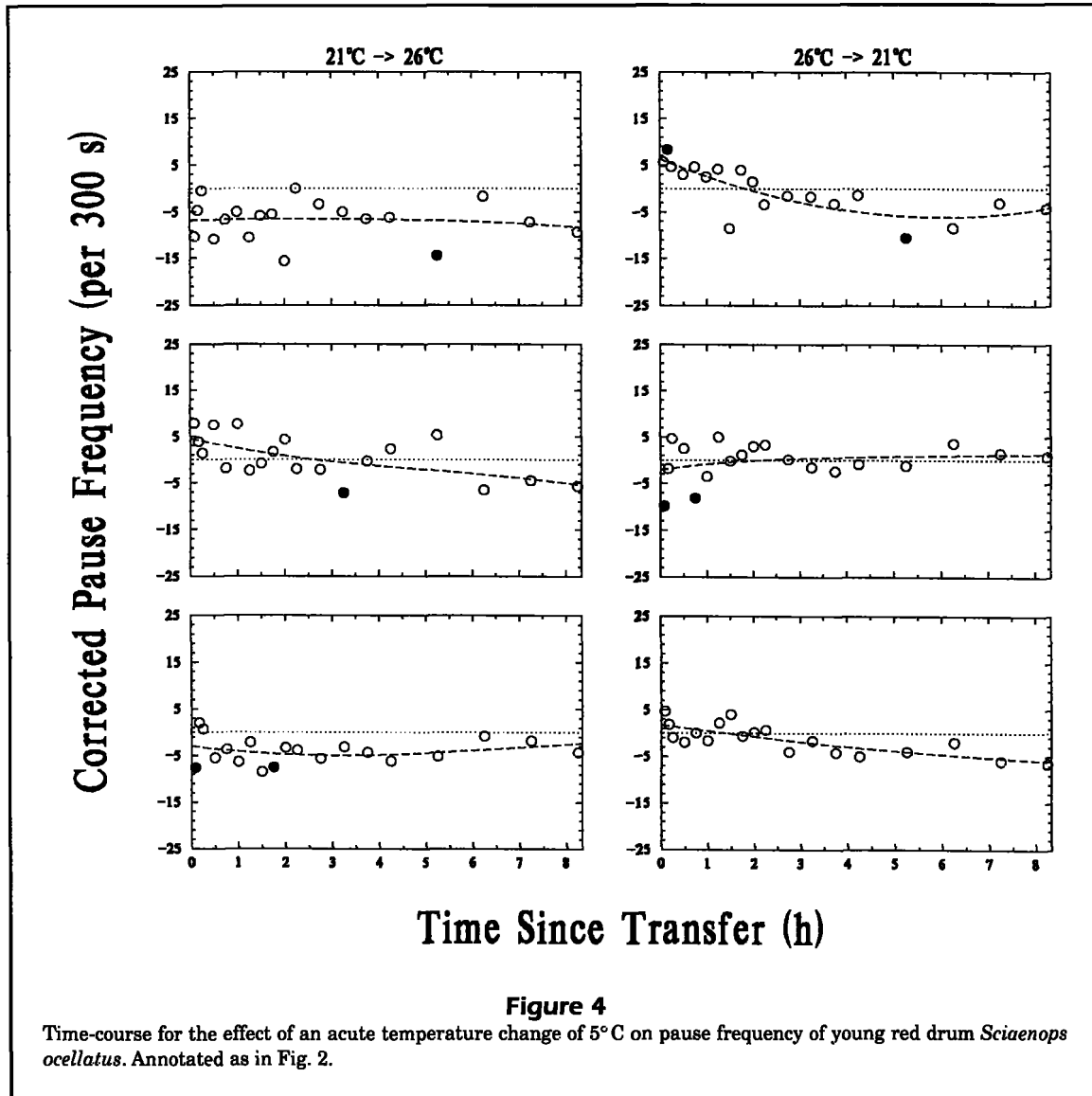
Activity of young red drum closely followed the traditional time-course at all sizes, whether the transfer was upward or downward. The general temporal trends in activity had similar shapes and values within treatments. Similar experiments conducted on a single size ('underyearlings') of Atlantic salmon also showed that spontaneous activity followed the overshoot model for adaptation (Peterson & Anderson 1969). Interestingly, activity of salmon did not decrease dramatically in downward transfers, as predicted. Rather, the time-course for activity followed trends similar to those resulting from temperature increases. Peak activity in the overshoot period correlated with the rate of temperature change, rather than the magnitude or direction of the change. Also, peak activity for salmon transferred to 12°C from 6°C was considerably lower than that for fish undergoing a similar downward transfer from 18°C. Our data show a similar relationship between the direction of transfer and mean peak (positive or negative) activity during the overshoot period. Upward transfers resulted in lesser overshoots of activity than downward transfers, and overshoot periods were later and prolonged. The differences were not as great as those found by Peterson & Anderson (1969)

for salmon, probably because of the smaller differences between acclimation temperatures in our experiments (5° vs. 12°C).

To our knowledge, no other investigators have examined the influence of acute temperature change on pause characteristics. Pause duration followed trends that were broadly similar to the overshoot model and consistent across sizes. Variability around the trends increased with size of fish. Unlike activity, peak pause duration was essentially independent of the direction of temperature change, but there were differences among sizes. Pause frequency showed fundamentally different time-courses. These were not consistently related to the direction of temperature change or fish size. Pause frequency obviously is not a good indicator of the state of thermal adaptation. Its lack of uniformity suggests that it is highly variable and may be influenced by numerous other factors.

Acclimation differences

Activity also exhibited the strongest and most consistent effects of different constant temperatures in young red drum. In control experiments, the pattern of activ-



ity over time followed similar trends at the two temperatures within each size-class, showing the same initial response in activity followed by stable behavior after 2–4 h. Once stabilized, the proportion of time spent actively swimming was 21–26% greater at the higher temperature. This is equivalent to a temperature coefficient (Q_{10}) of 1.5–1.6, which is similar to values reported for various other whole-animal measures of fish swimming. Maximum sustainable speed of carp has a Q_{10} of 1.5–1.6 (Rome et al. 1984). Larval zebra danio and Atlantic herring have temperature coefficients between 1.4 and 1.7 for burst distance and maximum burst speed (Fuiman 1986, 1991). Larger rainbow trout have values of 1.8 for burst distance (Webb 1978).

Stabilized activity (after 4 h) in the control experiments, combined with pause frequency, describe a temperature effect on the duration of active bouts between pauses. The average duration of active bouts is very nearly the ratio of total activity to pause frequency, since pause frequency is essentially equal to the number of active periods. Higher values for activity at the upper temperature, accompanied by lower or equivalent pause frequencies, result in longer periods of activity in warmer water. This effect holds for all three size-classes, although the magnitude of the effect is greatest for small fish.

All variables we evaluated relate to foraging activity, and since fish were not fed during the experiments, there should have been ample motivation for fish to

Table 3

Significance levels (P) for F tests in repeated-measures MANOVA of pause duration in red drum *Sciaenops ocellatus*. Boldface values indicate significant effects at $\alpha=0.05$. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic, 3=cubic).

Treatment	Effect	Size-class			
		All	Small	Medium	Large
All	Size	<0.001			
	Treatment	0.014			
	Time	<0.001			
Upward transfer	Size	0.027			
	Time	0.080	<0.001 ¹	0.174	0.410
Low control	Size	0.013			
	Time	<0.001	0.071	<0.001 ^{1,2,3}	0.420
Downward transfer	Size	0.039			
	Time	0.022	0.379 ²	0.024 ¹	0.729
High control	Size	0.183			
	Time	0.203	0.001	0.391	0.437
High control vs. low control	Treatment		0.062	0.033	0.202
	Time		0.001	<0.001	0.474
Upward transfer vs. low control	Treatment		0.134	0.224	0.500
	Time		0.009	<0.001	0.476
Downward transfer vs. high control	Treatment		0.035	0.036	0.026
	Time		0.310	0.011	0.781

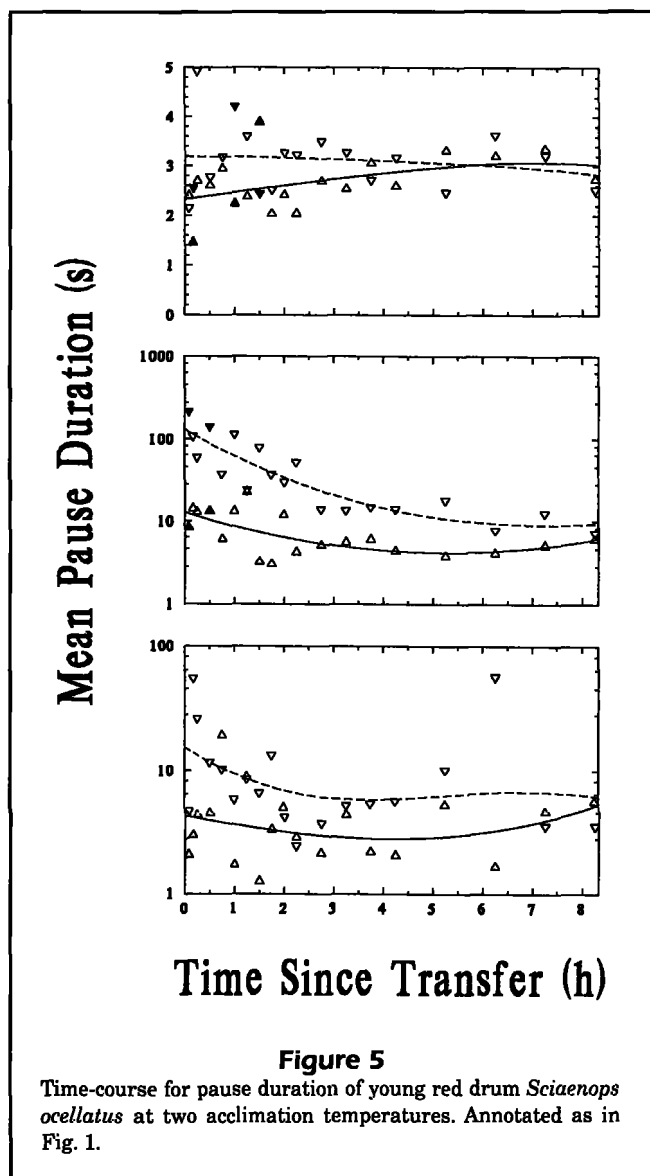
search for food once the effects of handling subsided. Fish in warmer water would be expected to have a higher demand for food at any time in the experiment due to a higher metabolic rate. Further, small fish should have a higher demand than larger fish. Increased demand for food should be met by an increase in the volume searched per unit time.

The means by which a fish increases the volume searched per unit time depends on the type of searching employed (i.e., sweep vs. saltatory). Search volume for sweep searchers is proportional to the distance traveled. A sweep searcher in warmer water should swim faster, for longer periods, and/or pause less often. For saltatory searchers, search volume is directly proportional to pause frequency. Saltatory searchers can scan greater volumes by increasing both pause frequency and swimming speed between pauses. In the absence of suitable prey, their pause duration should be constant and only as long as necessary to scan each field completely. Our results for total activity and mean bout duration from the stabilized levels of control experiments follow the pre-

dictions for a sweep searcher: In warmer water, activity is higher, pause frequency is shorter, and the duration of active bouts is longer. Predictions for a saltatory searcher are contradicted, since pause frequency is not higher in warmer water. In fact, the opposite is true for small fish, which should be most strongly affected by hunger.

Conclusion

Experimental conditions cannot mimic the various natural scenarios of transient temperature fluctuation. Diel temperature changes are usually gradual and predictable. Yet, even when acclimated to regular circadian cycles, swimming behavior may be influenced by ambient temperature (Fuiman 1986). Traversing a thermocline is more abrupt, but it is predictable and at least partly voluntary, allowing for some degree of physiological preparation. Such vertical migrations can be beneficial to a fish's daily energy budget (Brett 1971, Wurtsbaugh & Neverman 1988), but there may



be an immediate cost in terms of locomotor efficiency. Perhaps the most hostile type of natural temperature fluctuation is exemplified by inundation of tidal pools. It is both unpredictable and abrupt, and concomitant physical changes (e.g., sound and pressure) probably add to the thermal effects on behavior. Our results show that acute temperature changes of 5°C alone engender behavioral changes that persist for about 2 h. These changes may act directly on a fish's ability to forage normally, or they may be merely indicators of a generally stressed condition in which a fish could be more susceptible to predators or disease.

In addition to the thermal impacts, our fish exhibited a handling effect which was overcome in 3–5 h. The most similar circumstance experienced by young

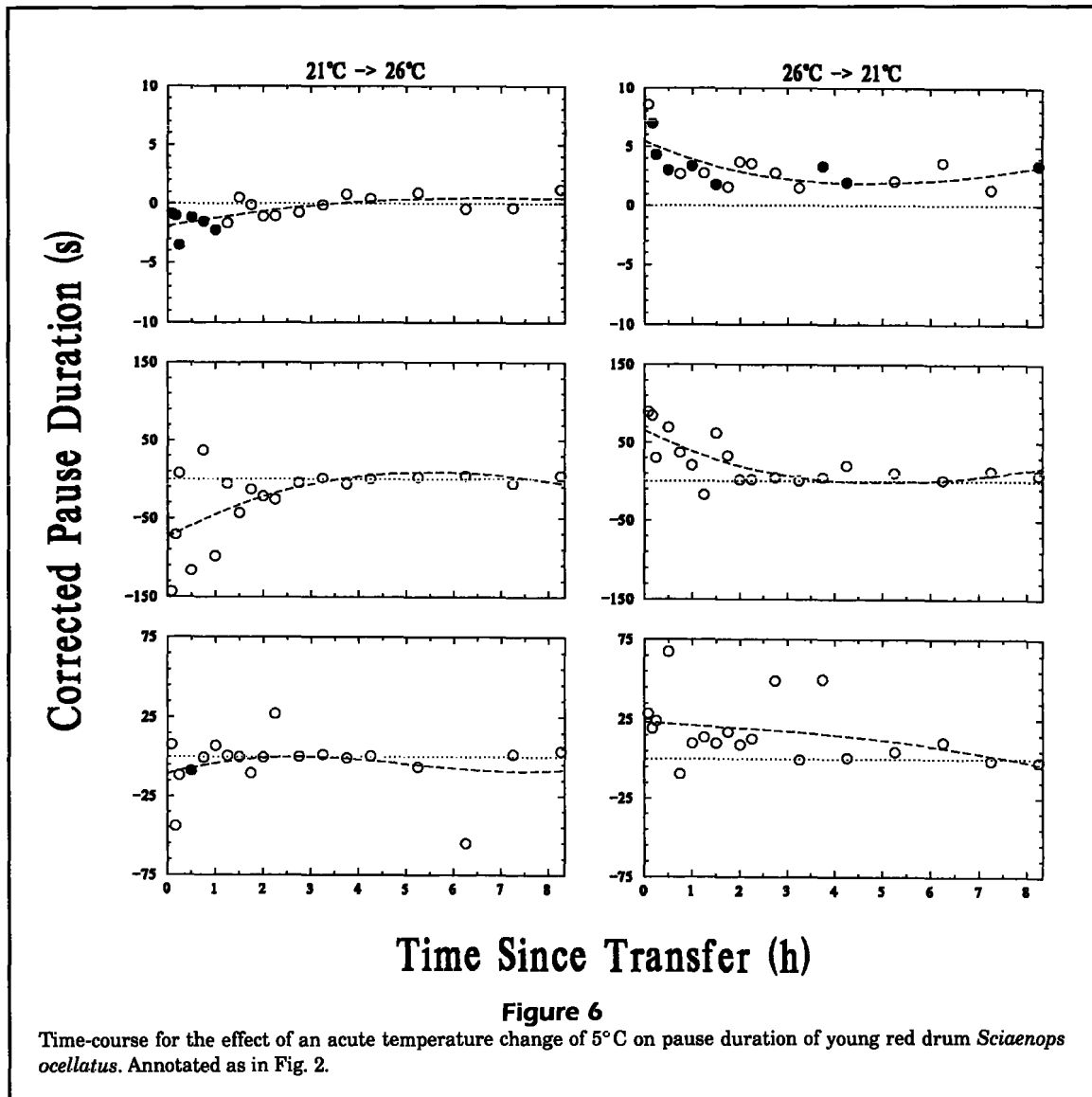
red drum in the field occurs during stocking from hatcheries into natural waters. Young red drum, 3–40 mm in length, have been stocked into bays and estuaries routinely since 1975 (Dailey 1991). Stocked fish experience the combined effects of handling and temperature change (often more than 5°C). Similarly, fish used in laboratory experiments often incur handling and thermal stress. Our results suggest that even careful handling affects behavior for at least as long as a 5°C temperature change. Minimal handling and an acclimation period of 2–5 h would benefit young red drum during both laboratory experiments and stocking.

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