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## Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats

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**Abstract** RNA:DNA ratios of larval and juvenile red drum (*Sciaenops ocellatus*) collected from nursery habitats in the Aransas Estuary, Texas, in 1994 were quantified using a highly sensitive ethidium-bromide fluorometric technique. RNA:DNA ratios of wild red drum were evaluated by comparing individual values to a linear regression model derived for starved laboratory-reared red drum. Wild red drum were in relatively good condition with <5% of the RNA:DNA ratios within or below the 95% prediction interval of 4 to 5 d starved red drum. A multiple-regression model explained 54% of the variability in the RNA:DNA ratio of wild red drum, and identified length and water temperature (midday) as significant factors. RNA:DNA ratios increased with fish length [ $\approx 1.1 \text{ mm}^{-1}$ , over the size range investigated (5 to 20 mm)]. The effect of temperature on the RNA:DNA ratio was assessed on different sampling trips, and ratios increased with increasing temperature. Abundance of larval and juvenile red drum in the Aransas Estuary varied as a function of both habitat (shoal grass *Halodule wrightii*, turtle grass *Thalassia testudinum*) and site (Aransas Bay, Redfish Bay); however, no differences in RNA:DNA ratios were detected between habitats or between sites. It is postulated that the nutritional condition of newly settled red drum from the Aransas Estuary in 1994 was relatively high, and that starvation was of minor importance.

### Introduction

Evaluation of the specific factors regulating life-history dynamics of marine fish populations is essential to un-

derstanding recruitment. Variability in recruitment is thought to be largely controlled by early life-history events (Cushing 1975; Sinclair 1988; Jones 1990). Expected survivorship from larval to juvenile stages is typically very low (<0.1%) and attributed primarily to predation and starvation (Houde 1987). Starvation and predation are interrelated processes, since poor nutritional condition reduces growth rates and results in prolonged larval stage durations (Buckley 1984). Thus, individuals spend more time in the size ranges most vulnerable to predators (Rice et al. 1993). Consequently, estimates of nutritional condition and growth during early life-history stages are crucial in determining an individual's probability of survival.

Several techniques (i.e. biochemical, morphological, histological) have been used as measures of nutritional condition and growth for larval and juvenile fishes (Ferron and Leggett 1994). The need for sensitive indicators has resulted in extensive research on biochemical techniques, particularly the use of nucleic acids. The quantity of ribonucleic acid (RNA) varies with the rate of protein synthesis, while the amount of deoxyribonucleic acid (DNA) per cell is a species-constant in somatic tissue. As a result, variations in the RNA:DNA ratio reflect changes in protein synthesis rates (i.e. growth). The RNA:DNA ratio has proven to be a useful indicator of nutritional condition and growth for a variety of larval fishes (e.g. Buckley 1979, 1980, 1981). RNA:DNA ratios of several species of larval fishes have been correlated positively with prey density (Buckley 1979; Buckley et al. 1984). Moreover, during periods of starvation, RNA:DNA ratios have been shown to decline (e.g. Wright and Martin 1985; Richard et al. 1991; Clemmesen 1994). Strong positive correlations between RNA:DNA ratios and growth rates have also been reported (Westerman and Holt 1994).

In the present study, we examined the RNA:DNA ratios of larval and juvenile red drum (*Sciaenops ocellatus*) from laboratory cultures and estuarine nursery habitats. The suitability of the RNA:DNA ratio as an index of nutritional condition and growth rate for red drum

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has been demonstrated in laboratory trials (Westerman and Holt 1994; Rooker and Holt 1996) and has led to investigations into the field application of the technique. The primary aim of this study was to evaluate the condition of newly settled red drum from estuarine nursery habitats in south Texas. RNA:DNA ratios of laboratory-reared red drum, under different nutritional states (i.e. fed vs starved), were compared to those of wild specimens, and a model was developed to determine the effects of biotic and abiotic factors on the RNA:DNA ratio. The quality of different nursery areas was also evaluated by examining spatial variations in condition (RNA:DNA ratio) and abundance of wild red drum.

## Materials and methods

### Laboratory experiments

Laboratory-reared red drum (*Sciaenops ocellatus*) were obtained from captive spawns (parental source: five wild-caught adults from the northwestern Gulf of Mexico) induced by photoperiod and temperature cues (Arnold 1988) at the University of Texas Marine Science Institute, Port Aransas, Texas. Eggs were treated with a 10 ppm formalin bath for 1 h and then placed in 150-liter cone-bottom, vertical tanks with internal biofilters (Holt 1993). Eggs hatched within  $\approx 24$  h, and larvae began feeding at 3 d post-hatch following the depletion of the yolk sac. After 20 d, larvae were transferred to a 1100-liter, modified v-bottomed raceway with removable partitions and an external biological filter (Holt 1992), located in a greenhouse. Larvae were fed live rotifers (*Brachionus plicatilis*) at a concentration of 3 to 5 ml<sup>-1</sup> from 3 to 12 d, and brine shrimp nauplii (*Artemia* sp.) at 1 to 2 ml<sup>-1</sup> from 10 to 25 d. Beyond 25 d, larvae and juveniles were fed a combination of yellowtail snapper (*Ocyurus chrysurus*) eggs and shrimp slurry. The laboratory was kept under controlled temperature and photoperiod conditions of 26 °C and 12 h light 12 h dark respectively. During the day,  $\approx 675 \mu\text{E m}^{-2} \text{ s}^{-1}$  light was available at the surface of the tanks. Salinity was maintained at 29‰ and total ammonia nitrogen below 0.5 ppm. Water-quality conditions in the greenhouse tank were similar to laboratory tanks; however, natural fluctuations in temperature (daily range  $\approx 24$  to 29 °C) and light occurred.

To evaluate the RNA:DNA ratio under varying nutritional states, starvation experiments were conducted on laboratory-reared red drum. Starvation periods were 5 d in duration and conducted at three ontogenetic stages ( $T_0 = 20, 30, 40$  d), where  $T_0$  represents the age (days post-hatch) prior to starvation (control). A sample of eight individuals was taken prior to starvation (0 d) as a control, and the remaining larvae were placed individually in 1-liter beakers with similar water conditions. A second control sample (fed larvae) was also taken at the end of trials that began on Days 20 and 30. No significant differences ( $P > 0.05$ ) in RNA:DNA ratios were detected between controls at 0 and 5d. Samples of eight red drum were collected daily from randomly selected beakers for 5 d. Red drum were sampled at 12:00 hrs each day. Survivorship during all starvation trials was  $>90\%$ .

### Field collections

Wild red drum were collected from estuarine seagrass meadows located in the Aransas Estuary, Texas (Fig. 1). Newly settled red drum were caught using an epibenthic sled measuring  $0.75 \times 1.0 \times 0.5$  m (length  $\times$  width  $\times$  height), equipped with a 500  $\mu\text{m}$ -mesh, conical plankton net. Collections were taken during the annual settlement period (September to November, 1994). Samples were collected from four stations located within Aransas Bay (ARB1,

ARB2) and Redfish Bay (RFB1, RFB2). At one station within each bay (ARB1, RFB1), co-occurring monotypic stands of the two primary seagrass meadows found in south Texas, shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*) were sampled separately to evaluate habitat effect. At each paired station, monotypic stands of both seagrass species were within 100 m of each other. Only shoal-grass habitats were sampled at the two other stations (ARB2, RFB2). In addition to habitat type and site, depth, water temperature, time of day, salinity, wind speed, wind direction, and water clarity were recorded.

### Nucleic acid determination

Red drum from both the laboratory and field were measured to the nearest 0.5 mm (standard length) and placed immediately on dry ice. Samples were stored at  $-80$  °C. Nucleic acid measurements were made on sections of trunk muscle. Samples were homogenized in 800  $\mu\text{l}$  ice-cold 1 M NaCl. Homogenates were immediately centrifuged at  $3000 \times g$  for 45 min at 4 °C. Aliquots (100  $\mu\text{l}$ ) were drawn for fluorometric analyses.

DNA and RNA measurements were made using the ethidium bromide (EB) fluorometric technique described by Westerman and Holt (1988, 1994). Aliquots of homogenates (100  $\mu\text{l}$ ) were used to estimate DNA and RNA values. Calculations were based on comparisons to DNA-EB and RNA-EB calibration curves from known standards. Calf thymus DNA and yeast RNA (Type III) were used as standards.

### Statistical analyses

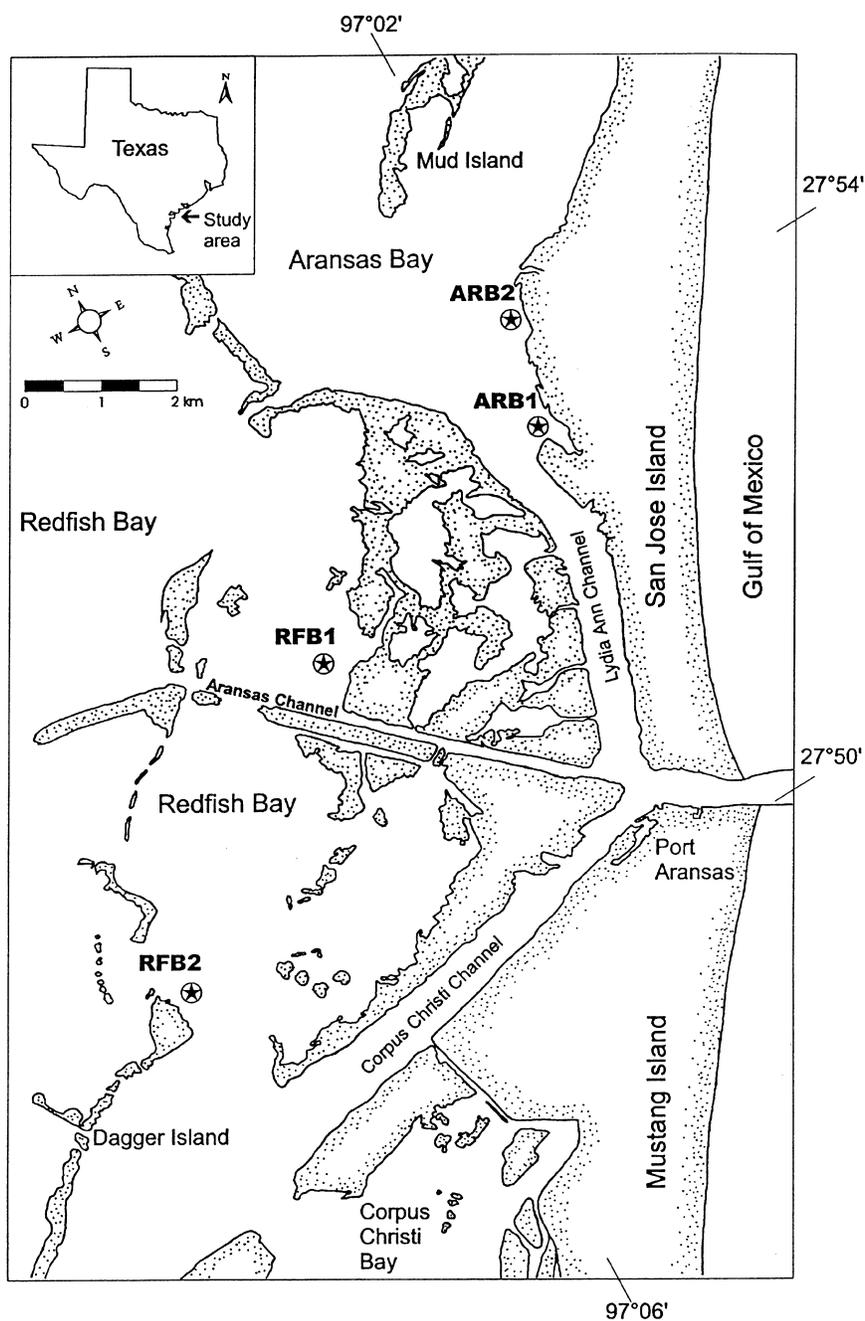
Analysis of variance (ANOVA) was used to examine the effect of starvation in laboratory trials. ANOVA results were further examined with Tukey's honestly significant difference (HSD) method to determine which levels of the main effect(s) differed significantly ( $\alpha = 0.05$ ) from other levels. A least-squares linear regression approach was employed to compare the condition of wild red drum to laboratory-reared specimens (Sokal and Rohlf 1981). Multiple-regression analysis was used to investigate the effects of biotic and abiotic conditions on RNA:DNA ratios. To reduce potential sources of bias (methods and field-related), the model was based on limited collections taken during peak recruitment (4 October to 7 November) and all individuals were assayed within a 1 wk period. Similarly, spatial variations in condition and abundance were assessed during this interval. Due to the influence of fish size, the effects of habitat and site on RNA:DNA ratios were investigated using an analysis of covariance (ANCOVA), where differences in the covariate (length) between habitats and sites were adjusted. ANOVA was also used to assess patterns in the spatial distribution of wild red drum. The software package SYSTAT (Wilkinson 1991) was used for statistical testing.

## Results

### Laboratory calibration

RNA:DNA ratios decreased continuously in larval and juvenile *Sciaenops ocellatus* over the 5 d starvation periods for all three ontogenetic stages (Table 1). Tukey's HSD test detected differences ( $P < 0.05$ ) in RNA:DNA ratios of fed and starved red drum within 1 or 2 d of food deprivation for all trials. RNA:DNA ratios of laboratory-reared fed and 4 to 5 d starved red drum as a function of length were compared (Fig. 2). Variability in the RNA:DNA ratios of fed (control) red drum was high. In contrast, variability for 4 to 5 d

**Fig. 1** Map of Aransas Estuary showing location of sampling sites in Aransas Bay (*ARB1*, *ARB2*) and Redfish Bay (*RFB1*, *RFB2*)



starved red drum was low and RNA:DNA ratios were close to the 95% prediction interval. The relationship between standard length (SL) and the RNA:DNA ratio for 4 to 5 d starved red drum was significant ( $P < 0.01$ ) and described by  $\text{RNA:DNA} = 1.171 + 0.330 \text{ SL}$  ( $r^2 = 0.42$ ). No overlap in RNA:DNA ratios between fed and 4 to 5 d starved red drum was observed.

#### Condition of wild red drum

The condition of wild red drum was evaluated by comparing RNA:DNA ratios to the linear regression model

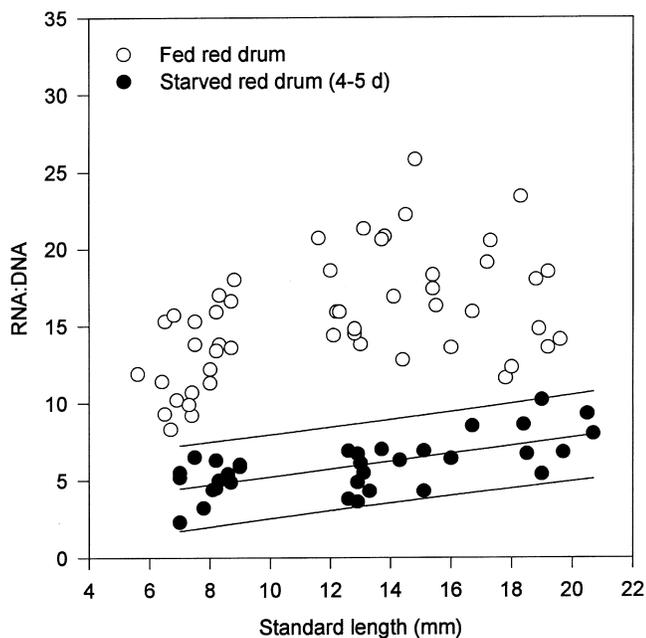
derived for 4 to 5 d starved laboratory-reared red drum. The RNA:DNA ratios of wild red drum were highly variable and the majority of points fell within or above the range of fed red drum (Fig. 3). Less than 5% of the RNA:DNA ratios of wild red drum were within or below the 95% prediction interval of 4 to 5 d starved red drum. The majority of red drum experiencing some level of starvation were  $<10$  mm.

A multiple-regression model that incorporated fish size and several environmental factors explained 54% of the variability in the RNA:DNA ratios of wild red drum. Length and temperature (midday) were the only significant ( $P < 0.01$ ) factors in the model (Table 2).

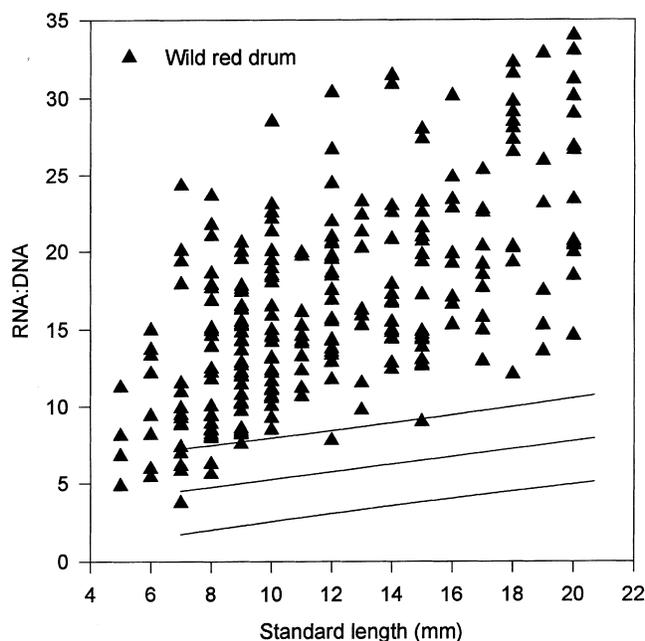
**Table 1** *Sciaenops ocellatus*. Variations in RNA:DNA ratios of fed (control) and starved larvae and juveniles. Starvation periods were 5 d in duration and conducted at three ontogenetic stages ( $T_0 = 20, 30, 40$  d [ $T_0$  day prior to starvation (control)]). Estimates are daily means based on 6 to 8 individuals  $\pm 1$  SE. Mean standard length (mm)  $\pm 1$  SE for  $T_0$  controls at 20, 30 and 40 d was  $8.0 \pm 0.2, 14.0 \pm 0.6,$  and  $22.9 \pm 1.2,$  respectively (<sup>\*</sup>RNA:DNA ratio differed from 0 day control (based on Tukey's HSD test))

Days starved	$T_0$ :		
	20 d	30 d	40 d
0 ( $T_0$ control)	$18.3 \pm 1.0$	$15.4 \pm 1.0$	$19.7 \pm 1.7$
1	$17.9 \pm 0.8$	$11.8 \pm 0.5^*$	$15.4 \pm 1.0$
2	$14.9 \pm 1.3^*$	$7.7 \pm 0.4^*$	$14.2 \pm 1.0^*$
3	$11.6 \pm 1.3^*$	$6.8 \pm 0.4^*$	$11.2 \pm 0.7^*$
4	$5.7 \pm 0.6^*$	$6.6 \pm 0.1^*$	$8.6 \pm 0.4^*$
5	$4.9 \pm 0.6^*$	$4.4 \pm 0.3^*$	$8.7 \pm 1.3^*$

Temperature at the time of collection, time of day, salinity and water clarity were not significant ( $P > 0.05$ ). To further investigate the effects of length and midday temperature, a stepwise multiple regression was used. Results from this analysis indicated that length was the most important predictor, accounting for 43% of the observed variability. Midday temperature was the next variable added to the model in the forward selection procedure, and together with length accounted for 52% of the variability in the RNA:DNA ratio.



**Fig. 2** *Sciaenops ocellatus*. RNA:DNA ratio as a function of standard length for fed (control) and 4 to 5 d starved laboratory-reared larvae and juveniles (fed  $n = 51$ ; 4 to 5 d starved  $n = 40$ ). Simple linear regression plot with 95% prediction interval shown for 4 to 5 d starved red drum



**Fig. 3** *Sciaenops ocellatus*. RNA:DNA ratio as a function of standard length for wild larvae and juveniles caught in Aransas Estuary in 1994 ( $n = 254$ ). Regression line and 95% prediction interval determined for 4 to 5 d starved red drum from laboratory trials are included

RNA:DNA ratios of wild red drum were positively correlated with length. Mean RNA:DNA ratios ranged from 7.73 in 5 mm larvae to 25.90 in 20 mm juveniles. A linear regression of standard length on the mean RNA:DNA ratio (per mm size class) indicated that the ratio increased by  $\approx 1.1$  for each mm increase in length ( $y = 3.417 + 1.086x$ ;  $r^2 = 0.94$ ).

The effect of temperature on the RNA:DNA ratio was evaluated during peak recruitment on four sampling dates characterized by different midday temperatures: 4 October (29 °C), 11 October (21 °C), 24 October (28 °C), 7 November (23.5 °C). To adjust for the influence of length, a linear regression was calculated for the

**Table 2** *Sciaenops ocellatus*. Environmental parameters included in multiple-regression model for evaluating effects on RNA:DNA ratios of wild larvae and juveniles from Aransas Estuary ( $n = 144$ ,  $r^2 = 0.54$ ) [(1), (2) midday (12:00 hrs) temperature and collection temperature, respectively;  $t$  Student's  $t$ -statistic]

Variable	Coefficient (SE)	Standard	$t$	$P$
		coefficient		
Standard length	1.143 (0.123)	0.645	9.256	< 0.001
Temperature (1)	1.826 (0.488)	0.639	3.739	< 0.001
Time of day	0.009 (0.005)	0.269	0.178	0.053
Temperature (2)	-0.824 (-0.546)	0.235	-1.509	0.134
Salinity	0.366 (0.470)	0.091	0.780	0.437
Water clarity	0.570 (1.214)	0.047	0.341	0.640

RNA:DNA ratio (ln-transformed) as a function of standard length. Residuals from this regression were then plotted against temperature and showed a significant ( $P < 0.01$ ) positive correlation. Thus, RNA:DNA ratios were greater at higher temperatures. RNA:DNA ratios increased by approximately 1.0 per centigrade increase.

#### Spatial variations in abundance and condition

Relationships between red drum abundance in estuarine nursery habitats and RNA:DNA ratios were also examined during peak recruitment (4 October to 7 November). Abundance (individuals  $m^{-2}$ ) of larval and juvenile red drum varied significantly (ANOVA,  $P < 0.01$ ) between sites (Table 3). Mean abundances from shoal-grass habitats located in Aransas Bay and Redfish Bay were 1.86 and 0.69  $m^{-2}$ , respectively. However, ANCOVAs (based on pooled stations) showed that RNA:DNA ratios did not vary significantly between sites ( $P > 0.05$ ). A trend in the relative abundance of red drum was also observed between habitats. In paired comparisons at Aransas Bay (ARB1) and Redfish Bay (RFB1), red drum abundances were higher in shoal-grass (1.82 and 1.24  $m^{-2}$ , respectively) than in turtle-grass (0.73 and 0.33  $m^{-2}$ , respectively) habitats, with >70% of all red drum being collected from shoal-grass beds. However, ANCOVAs indicated that RNA:DNA ratios did not differ significantly ( $P > 0.05$ ) between shoal- and turtle-grass habitats.

To adjust for the influence of temperature on the RNA:DNA ratio, we also analyzed two collection dates separately (i.e. no temperature effect) using ANCOVAs. Similar to the above findings, RNA:DNA ratios of red drum were not significantly ( $P > 0.05$ ) different between habitats or between sites.

#### Discussion

The aim of this study was to evaluate the condition of wild larvae and juveniles of *Sciaenops ocellatus* using the RNA:DNA ratio. Our assessment was dependent on the assumption that the RNA:DNA ratio was a suitable measure of condition. Results from laboratory trials on red drum established a strong relationship between the RNA:DNA ratio and nutritional condition (fed vs starved) and provided a frame of reference for evaluating the condition of wild red drum.

The effect of starvation on the RNA:DNA ratio has been reported in numerous studies (e.g. Buckley 1980, 1981; Clemmesen 1987, 1994; Richard et al. 1991). In general, RNA:DNA ratios decline during starvation, resulting from a decrease in the muscle quantity of ribosomal RNA and the reduced efficiency of amino acid incorporation (Ferron and Leggett 1994). Clemmesen (1994) reported that fed and starved herring (*Clupea harengus*) larvae (>10 d) could be distinguished after 3 to 4 d. Further food deprivation resulted in a continued decline in RNA:DNA ratios. Similarly, Richard et al. (1991) reported that fed and starved larval and juvenile sole (*Solea solea*) could be discriminated within a few days using RNA:DNA ratios. Data presented in the present study for larval and juvenile red drum corroborate these findings. RNA:DNA ratios of laboratory-reared red drum decreased soon after the start of starvation, and differences between fed and starved individuals were statistically significant within 1 to 2 d of food deprivation.

Since starvation is easier to define than good feeding under laboratory conditions, the nutritional condition of wild red drum was evaluated by comparing RNA:DNA ratios to starved individuals. RNA:DNA ratios of red drum from estuarine nursery habitats suggest that starvation was of minor importance to newly settled individuals in the 1994 year-class. In fact, <5% of all individuals assayed had RNA:DNA ratios within or below the prediction interval maintained by 4 to 5 d

**Table 3** *Sciaenops ocellatus*. Mean abundance (individuals  $m^{-2}$ ) of larvae and juveniles collected from demersal seagrass habitats in Aransas Estuary, Texas (1994). Estimates are given by habitat, site, and collection date. Abundance estimates per cell based on 6 and 3 replicate sled tows for shoal grass (*Halodule wrightii*) and turtle grass (*Thalassia testudinum*), respectively

Collection date	Shoal grass ( <i>H. wrightii</i> ) <sup>a</sup>			Turtle grass ( <i>T. testudinum</i> ) <sup>b</sup>		
	Aransas Bay	Redfish Bay	(Mean)	Aransas Bay	Redfish Bay	(Mean)
04 Oct	1.65	0.10	(0.87)	–	–	
11 Oct	1.27	2.22	(1.74)	0.51	0.62	(0.57)
17 Oct	1.31	0.28	(0.80)	–	–	
24 Oct	1.68	0.38	(1.03)	0.29	0.09	(0.19)
31 Oct	3.05	0.86	(1.95)	–	–	
07 Nov	2.24	0.31	(1.27)	1.38	0.27	(0.83)
Mean (all dates)	1.86	0.69	(1.28)	0.73	0.33	(0.53)

<sup>a</sup>Estimates based on pooled stations: Aransas Bay (ARB1, ARB2), Redfish Bay (RFB1, RFB2)

<sup>b</sup>Estimates from a single station: Aransas Bay (ARB1), Redfish Bay (RFB1)

starved larvae. It is important to note that the 4 to 5 d starvation period is considered moderate to severe, depending on the size of the individual. In general, the point of no return (PNR) for small red drum larvae (6 to 10 mm SL) is  $\approx$ 6 to 8 d, while larger individuals (15 to 20 mm SL) can survive 14 to 16 d without food (G. J. Holt unpublished data).

Starvation-induced mortality is often implicated as an important component in the larval fish paradigm (e.g. Houde 1977; Theilacker 1986; Cushing and Horwood 1994), particularly during the "critical period" when larvae convert from yolk nutrition to exogenous sources (Hjort 1914). However, once larvae move from offshore planktonic to inshore demersal habitats, prey abundance often increases (Rudnick et al. 1985), due primarily to increased productivity and structural complexity of inshore habitats (Giere 1993). Therefore, the enhanced supply of prey resources present in estuarine nursery zones may lessen the likelihood of starvation. Houde (1978) reported critical food concentrations for three species of subtropical marine fishes on the order of  $10^4$  to  $10^5$  zooplankton  $m^{-3}$ . Concentrations of epibenthic adult copepods, the primary prey taken by larval red drum (Peters and McMichael 1987), in the Nueces Estuary (adjacent to the Aransas Estuary) range from 3 to  $4 \times 10^5$   $m^{-2}$  surface substrate (Montagna and Kalke 1992). This range is a conservative estimate of prey availability, since it is based only on epibenthic prey (excludes copepods in the water column) and collections were taken from sites without seagrass; epifaunal abundance and above-ground seagrass biomass are often positively associated (e.g. Stoner 1980; Orth et al. 1984). Consequently, prey resources for larval and juvenile red drum in demersal habitats appear to be abundant, and starvation-induced mortality is probably low.

The interpretation that starvation is inconsequential during early demersal stages may be biased if predators are selectively removing red drum in poor condition. Recent studies have suggested that starvation could intensify predation mortality (Folkvord and Hunter 1986; Gamble and Fuiman 1987). Ivlev (1961) showed that predation rates on roach larvae (*Rutilus rutilus*) by young pike (*Esox lucius*) were positively associated with duration of starvation of the prey. Moreover, other studies have demonstrated that escape swimming speed and response rates to stimulation are compromised by starvation (Rice et al. 1987; Yin and Blaxter 1987). Conversely, starvation may actually enhance survival if changes in behavior (swimming speed and pause duration) make prey less conspicuous to predators (i.e. reduced encounter rate). Thus, it is difficult to quantify the sublethal effects of starvation and how they relate to predation mortality.

A variety of environmental factors have been associated with changes in biochemical condition. Biotic factors include food availability (Ferron and Leggett 1994), ontogenetic stage (e.g. Clemmesen 1994; Westerman and Holt 1994; Rooker and Holt 1996), parental

source (Zastrow et al. 1989; Buckley et al. 1991a,b), diel periodicity (Mugiya and Oka 1991; Arndt et al. 1994; Rooker and Holt 1996), and disease (Steinhart and Eckmann 1992). Abiotic factors are generally associated with water quality and include temperature (Buckley 1982, 1984; Buckley et al. 1984, 1990; Jürss et al. 1987; Mathers et al. 1993), dissolved oxygen (Peterson and Brown-Peterson 1992), and toxicants (Kearns and Atchison 1979; Barron and Adelman 1984). In the present study, length and temperature (midday) were identified as important sources of variation. A predictive model based on these variables explained 52% of the variability in the RNA:DNA ratios of wild red drum. The addition of other environmental variables had no significant influence on the RNA:DNA ratio.

Similar to studies on other species (e.g. Buckley 1981; Richard et al. 1991; Clemmesen 1994), RNA:DNA ratios of wild red drum increased with length. Westerman and Holt (1994) suggested that increases in RNA:DNA ratios during early ontogeny are probably related to rapid cell division and increasing cell size (hypertrophy). RNA:protein and DNA:protein concentrations for red drum have been shown to decrease exponentially during early development (Rooker and Holt 1996), indicating that cell size is increasing. From limited data, we also observed that RNA:DNA ratios for red drum  $>20$  mm showed no length-dependency. These findings suggest that cell size increases during early ontogeny and, at  $\approx 20$  mm, growth at the cellular level becomes uniform. Fukuda et al. (1986) achieved similar results for Pacific herring (*Clupea pallasii*) larvae. Metabolic and physiological processes were nonuniform and affected by age and length in smaller larvae. Once larvae reached 30 mm, cellular processes became relatively uniform and metabolic balance was achieved.

RNA:DNA ratios also increased with increasing temperature for wild red drum, suggesting that protein synthesis rates were influenced by temperature. A relationship between temperature, protein growth, and the RNA:DNA ratio is expected, because RNA makes up the cell's protein synthesis machinery and temperature controls the rate of protein synthesis (Fry 1971). Most studies have reported that growth rates are positively affected by temperature, but the relationship between temperature and the RNA:DNA ratio is often variable and less conclusive, since compensatory mechanisms may be operating when temperatures are outside optimal ranges. In larval winter flounder [*Pleuronectes* (= *Pseudopleuronectes*) *americanus*] and sand lance (*Ammodytes americanus*), growth rates are higher at higher temperatures, but RNA:DNA ratios are not temperature-dependent (Buckley 1980, 1984). In larval plaice (*Pleuronectes platessa*), both growth rate (otolith and somatic) and RNA:DNA ratios are positively correlated with temperature (Hovencamp and Witte 1991). Juvenile rainbow trout (*Oncorhynchus mykiss*) show higher growth rates when water temperature is raised, but RNA:DNA ratios decrease with increasing water temperature (Mathers et al. 1993).

Since RNA:DNA ratios are sensitive to changes in feeding activity (Buckley 1979, 1980, 1984; Wright and Martin 1985; Clemmesen 1987), it is reasonable to assume that temperature-induced changes in feeding rates will affect the RNA:DNA ratio. Feeding rates of juvenile weakfish (*Cynoscion regalis*) increase significantly with temperature, ranging from  $\approx 10$  to 14% body wt  $d^{-1}$  at 20 °C to 33 to 39% body wt  $d^{-1}$  at 28 °C (Lankford and Targett 1994). In addition, Fuiman and Ottey (1992) examined the spontaneous behavior of larval and juvenile red drum exposed to different acclimation temperatures and observed that swimming activity of red drum acclimated at 26 °C was greater than at 21 °C. They suggested that increased swimming activity associated with increasing temperatures may increase the volume searched and, thus, feeding success would be enhanced. Temperature changes encountered by red drum during this study were within the optimal range (22 to 28 °C). Consequently, higher temperatures permitted increased feeding rates and faster growth rates, which were reflected in RNA:DNA ratios.

Spatial variations in red drum abundances were observed, but patterns were unrelated to differences in biochemical condition. Since larval size and stage duration are important determinants of survival (Houde 1987), individuals should reside in habitats that maximize growth. Sogard (1992) found that winter flounder densities matched growth patterns (i.e. areas with higher densities had higher growth). However, she also observed that highest natural densities of naked goby (*Gobiosoma bosc*) were present in the poorest habitat for growth. When fish densities do not match growth patterns, it is assumed that compromises or tradeoffs are occurring because survival is enhanced when individuals reside in habitats that maximize the ratio of growth to mortality (G:Z) (Werner and Gilliam 1984). Since RNA:DNA ratios (i.e. condition-growth) of wild red drum did not differ between habitats or sites, other components of habitat quality, not directly assessed in this study (i.e. protection from predators, stability), may influence habitat selection.

In summary, this study has demonstrated the potential usefulness of RNA:DNA ratios for assessing the condition of natural red drum populations; however, it requires certain precautions. Since RNA:DNA ratios of red drum are length- and temperature-dependent, standardization of biochemical measures is necessary to eliminate these known sources of variation. Using a laboratory calibration of starved red drum, it is postulated that the nutritional condition of newly settled red drum in 1994 from estuarine nursery habitats was relatively high, and starvation was of minor importance.

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