Abstract.—Oxygen consumption and nitrogen excretion rates were determined by direct measurement in fed and starved red drum, *Sciaenops ocellatus*, larvae between the ages of two and eighteen days. Oxygen consumption rates (Y, μL O_2/ind./h) scaled isometrically with mass (X, mg) according to the equation $Y = 4.58X^{1.04}$ (r^2=0.80) in larvae fed 5 prey/mL, resulting in a dry mass-specific oxygen consumption (QO_2) of 4.18 μL O_2/mg DM/h at a mass of 100 μg. In contrast, oxygen consumption of starved larvae scaled with mass according to the relationship $Y = 1.00X^{0.697}$ (r^2=0.50), resulting in a QO_2 of 2.01 μL O_2/mg DM/h at 100 μg. The 50% drop in QO_2 between fed and starved larvae over the mass range addressed in the study was assumed to represent the metabolic cost of growth (specific dynamic action).

Nitrogen was excreted in the form of ammonia and urea. Ammonia excretion (Y, μg NH_3/ind./h) varied with mass (X, mg) in fed individuals according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58), resulting in a dry mass-specific ammonia excretion rate of 0.52 μg NH_3/mg DM/h at a mass of 100 μg. Like oxygen consumption, nitrogen excretion in starved individuals dropped to 50% of that in fed animals, suggesting a general metabolic slowdown during starvation. Urea production as a percentage of total N-excretion was inversely related to ammonia production in starved individuals and increased with time of starvation; it may be an indicator of starvation in very young fish.

The isometric scaling of metabolism with mass in young larvae suggests that physiological vulnerability, i.e. susceptibility to starvation, does not decline rapidly with increasing size in young fish larvae. Larger larvae are nearly as vulnerable to starvation as smaller ones though their ecological position has improved, i.e. their predator spectrum has declined and their prey spectrum has increased.

Manuscript accepted 10 June 1996.
Fishery Bulletin 94:756–765 (1996).

Energetics of larval red drum, *Sciaenops ocellatus*. Part I: Oxygen consumption, specific dynamic action, and nitrogen excretion

Joseph J. Torres
Ross I. Brightman
Joe Donnelly
John Harvey

Department of Marine Science, University of South Florida
140 Seventh Ave South, St. Petersburg, Florida 33701
e-mail address: jtorres@marine.usf.edu

Energy utilization during a fish's early life history reflects its strategy for survival. Ingested energy must be apportioned between metabolic requirements and the need for growth in size; the remainder is lost as fecal and nitrogenous waste. The need for rapid growth in very young larvae is particularly critical: increasing size rapidly decreases the spectrum of potential predators even as it increases the spectrum of items available for forage (Weatherly and Gill, 1987). The two factors that most profoundly influence the amount of ingested energy available for growth are the energy lost to respiration and excretion (Brett and Groves, 1979; Houde, 1989).

Respiration in eggs and larvae is believed to occur through cutaneous diffusion (de Silva, 1974). At hatching, most species of fish lack respiratory pigments and are almost transparent. The blood of these larvae becomes pink weeks or months later upon transformation, which marks the time of blood pigment development and advanced gill filament formation (Weihs, 1981; Blaxter, 1986). Energy demands of respiration in fish larvae are temperature-dependent, ranging from 48% of the gross ingested food energy at 10°C to 31% at 30°C (Houde, 1989).

A portion of the food energy ingested by an individual is indigestible and lost as feces (up to 20% in older fish; Brett and Groves, 1979). In larval fishes, feces are small, difficult to collect, and, as a consequence, are rarely measured. The fraction of ingested energy lost to fecal excretion is therefore usually computed by the difference between the sum of the energy devoted to growth and metabolism and that ingested. Of the remaining food energy that is digestible, a portion is lost as nonfecal nitrogen, mainly as ammonia and urea. Brett and Groves (1979) have stated that energy lost through nonfecal excretion ranges from 3% to 10% of total ingested calories in adults. However, data describing nitrogen excretion in young fish larvae are very scanty. Available figures suggest that total excretion ranges from 23% to 40% of the gross ingested energy (Houde, 1989).

Data collected simultaneously on oxygen consumption and ammonia excretion can be used to determine the biological substrate that is combusted as fuel by using the atomic ratio of oxygen consumed to nitrogen produced (O:N ratio) (Davenport et al., 1983). The O:N ratios of 8 or less indicate that pure protein

is being combusted. Values higher than 20 suggest that lipids are the primary source of energy (Bayne, 1973). Larvae depleting their yolk-sac lipid reserves should thus exhibit high O:N values, whereas fast-growing larvae actively synthesizing protein with little or no lipid deposition or combustion should have low O:N values.

The aims of this study were to determine the respiratory costs of red drum larvae in their first 2 weeks of life, to determine the amount of energy lost as nitrogenous waste in the form of ammonia and urea, to determine the effects of starvation on both nitrogen excretion and respiration, and to determine, by using O:N ratios, the main biological fuel being combusted for energy.

Methods and materials

Maintenance of specimens

Fertilized eggs were obtained from the Florida Department of Environmental Protection (FDEP) hatchery in Port Manatee, Florida. Broodstock was maintained at a temperature of 25°C and a salinity of 30‰. Eggs were obtained from six spawnings over the course of six months to complete the respiration and excretion experiments described below.

Eggs were transported to the University of South Florida Marine Science Laboratory in St. Petersburg, and 2,500–3,000 individuals were placed into each 26-L experimental aquarium. The high mortality associated with first-feeding (cf. Roberts et al., 1978) resulted in a concentration of 250–300 individuals per aquarium after the first 3 days of life. Aquaria were kept in a photoperiod- and temperature-controlled incubator; water was maintained at 25°C and 30‰. A 13-hour light and 11-hour dark photoperiod was used throughout all experiments. Larvae were fed rotifers (*Brachionus plicatilis*) starting at day 3 after hatching until transformation (approximately day 14), when experiments were terminated. Aquaria were aerated and 10% of the water in each was changed daily.

Rotifers were cultured by using the procedure of Hoff and Snell (1987). Seawater for culturing was obtained from offshore in the Gulf of Mexico. The seawater was coarse-filtered, treated with bleach (sodium hypochorite, 5.25%) to remove any additional plankton, and neutralized with sodium thiosulfate. Salinity was adjusted with distilled water and Tropic Marine Seasalt to achieve a final salinity of 30‰.

Rotifers were provided at 5.0 per mL from first feeding (day 3) through day 14. Prey concentrations were monitored twice daily by removing a 25-mL sample from each aquarium, counting the number of prey in 0.5-mL aliquots, and taking the average. Concentrations were adjusted to maintain prey concentrations as necessary.

Oxygen consumption rate

Oxygen consumption was measured in red drum larvae ranging in age from 3 to 18 d. Individuals used in respiratory determinations were of two types: those fed ad libitum and those that had been starved for 24 h. Oxygen partial pressure was monitored in respiratory chambers with both "micro" and "needle" polarographic oxygen electrodes (Mickel et al., 1983; Revsbech and Ward, 1983) as individuals or groups of individuals reduced the oxygen levels to low (0–40 mm Hg) partial pressures. Cathode diameters on both the micro- and needle electrodes were sufficiently small to preclude the need for stirring; both types were manufactured in our laboratory. Starved individuals were monitored with the needle electrodes and fed larvae were monitored by both micro and needle electrodes. Electrodes were calibrated before and after each experimental run with air- and nitrogen-saturated seawater.

Respiratory chambers were manufactured from plastic 1-mL and 10-mL syringes. Each chamber was filled with seawater filtered through a 0.45 μm millipore filter and capped with an electrode fitted with an O-ring. The respiratory chamber within the syringe barrel was thus defined at one end by the syringe plunger and at the other end by the oxygen electrode. Single individuals were run by using a 1-mL syringe and the needle electrode set-up. Groups of 2 to 4 individuals were run in 10-mL syringes with a micro-electrode. Chambers were kept at 24 (±1.0)°C.

Data were continuously recorded throughout each run with either a computer-controlled data logging system (micro-electrodes) or a chart recorder (needle electrodes) (Donnelly and Torres, 1988). For data acquired with the chart recorder, the oxygen consumption rates were computed directly from the slope of the recorded data. Rates were calculated from the data-logger by noting the oxygen depletion over 10-min intervals. Typically, the first 30 min of a run were characterized by a high rate because of excitement associated with introduction into the respirometer. Thus, in all cases, data acquired during the first 30 min of the run were discarded. A mean respiratory rate for each run was determined by taking a mean of all the 10-minute rates comprising the run after the first 30 min. The lowest and highest 10-min rates for each run were designated the minimum and maximum rates.

After each run, individuals were rinsed with distilled water and dried at 60°C for 24 h, then weighed

with a Cahn Electrobalance for dry mass measurements. It should be noted that the number of replicate experiments for larvae starved for 24 h was lower than that for fed individuals because many of the larvae that survived the period of starvation were not hardy enough to be good experimental subjects.

Oxygen consumption as μL O_2 was converted to calories (cal) by using the oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves, 1979). Calories were then converted to joules (J) by multiplying by 4.1868 J/cal (Pennycuick, 1988).

Nitrogen excretion

Nitrogen excretion rates were determined for larvae of the same ages and feeding states as those used in the oxygen consumption experiments. Larvae aged 3 to 14 d were split into 2 feeding groups: those fed to satiation and those starved for 24 h. Five sets of 10 larvae were removed from each feeding group and each set was placed in a 10-mL screw-top centrifuge tube filled with seawater that had been filtered through activated charcoal. To measure any ammonia addition caused by transfer of the larvae, an additional tube was filled with charcoal-filtered seawater, and a volume of water from the incubation bowl equivalent to that associated with transfer of the larvae was added. A second additional tube was filled with 10 mL of charcoal-filtered seawater to serve as a blank.

All tubes were sealed and incubated for 4 h at 25°C. Larvae were subsequently filtered from the tubes with 50-μm mesh netting, dried at 60°C for 24 h, and weighed. The remaining sample water was split into 10-mL aliquots and immediately capped and frozen for later analysis. Concentrations of ammonia and urea for each sample were determined colorimetrically with an Alpkem autoanalyzer (Price and Harrison, 1987).

O:N ratios

O:N ratios (mol/mol) were calculated by using mass-specific oxygen consumption rates and our data for mass-specific total nitrogen excretion (ammonia and urea). Rates of mass-specific ammonia excretion were used to obtain O:NH_3 ratios.

Results

Oxygen consumption rates

Absolute oxygen consumption rates for individuals (ind.) fed 5.0 rotifers/mL increased with increasing dry mass and, as a consequence, with the age of the larvae as well (Table 1: Fig. 1). Rates ranged between 0.05 (day 3) and 0.14 μL O_2/ind./h (day 7) for the first week of growth. During the second week of growth, values increased sharply from 0.14 to 0.34 μL O_2/ind./h at day 14, reaching 0.77 μL O_2/ind./h at 18 d after hatching. The slope (b) of the oxygen consumption versus mass curve was 1.04 ±0.08 ($\bar{x}$ ±SE), indicating that metabolism was directly proportional to mass (isometric scaling) for the first two weeks of life. Mass-specific oxygen consumption (QO_2) varied between 2 and 6 μL O_2/mg DM/h with a mean of 4.23 ±0.17 μL O_2/mg DM/h ($\bar{x}$ ±SE). The slope (b) of the regression line for oxygen consumption versus age was 1.28 ±0.12.

Individuals starved for 24 h also had absolute oxygen consumption rates that increased with mass and age, but with lower b values (Fig. 2). Slope (b) for the oxygen consumption vs. mass curve dropped to 0.697 ±0.230 ($\bar{x}$ ±SE); that for oxygen consumption vs. age dropped to 0.975 ±0.400 ($\bar{x}$ ±SE). Absolute and mass-specific oxygen consumption and, as a consequence, energy utilization of starved larvae was one-half or less that of fed larvae at all ages up to day 17 (Table 2).

Table 1

Oxygen consumption of red drum, *Sciaenops ocellatus*, larvae fed at 5.0 prey/mL. n = number of sample runs; MDM = mean dry mass in μg; QO_2 = mass-specific oxygen consumption in μL O_2/mg DM/h; and ( ) = standard deviation.

Day	n	MDM	μL/ind./h	Mean QO_2	Min QO_2	Max QO_2
3	6	17.0	0.0473	2.78 (0.93)	1.15 (0.43)	4.56 (0.65)
4	4	24.1	0.1128	4.68 (1.02)	2.54 (1.38)	7.48 (1.71)
7	2	31.5	0.1402	4.45 (2.59)	1.53 (1.35)	11.70 (3.30)
8	4	34.1	0.1238	3.63 (1.73)	1.35 (1.17)	8.28 (2.79)
9	8	46.1	0.2466	5.35 (1.47)	2.01 (1.13)	11.10 (6.27)
10	5	52.0	0.2844	5.47 (0.83)	3.22 (1.46)	8.91 (3.85)
12	6	68.6	0.2593	3.78 (1.94)	1.24 (0.33)	10.80 (2.79)
14	6	109.0	0.3412	3.13 (1.56)	1.20 (0.54)	8.08 (3.18)
17	2	155.0	0.7316	4.72 (2.63)	1.46 (0.05)	12.40 (7.61)

Nitrogen excretion rate

Absolute ammonia excretion rates (Y, μg/ind./h) increased with increasing mass (X, mg) in larvae fed to satiation according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58) (Fig. 3). The slope of the excretion vs. mass curve in fed larvae (0.728) indicates that mass-specific ammonia excretion declines with increasing mass.

The relation between ammonia excretion and mass was substantially changed with a 24-h period of starvation, such that $Y = 0.058X^{0.328}$ (r^2=0.40) (Fig. 4). The change indicates that absolute ammonia excretion in starved individuals is roughly 50% that of fed individuals. In addition, the decline in mass-specific ammonia excretion with increasing mass is more pronounced as is indicated by the lower slope (0.328).

The increasing mass of growing larvae fed to satiation resulted in an increase in absolute ammonia excretion with age (Fig. 3). Starvation resulted in about a 50% decline in the slope of the relationship between excretion and age, similar to that observed in excretion vs. mass.

The percent contribution of ammonia and urea to total excretion differed; urea dominated in starved individuals. Urea in starved larvae (as total N excreted) was twice that of fed larvae (Table 3).

O:N ratios

The low O:N ratios based on both ammonia-N (O:NH_3) and total nitrogen (ammonia-N and urea-N) excretion rates indicated that protein was the combusted fuel (Table 4). O:NH_3 ratios ranged between 4 and 12 for all ages. O:N values based on combined ammonia-N and urea-N excretion were lower, ranging between 1 and 9. Larvae starved for 24 h

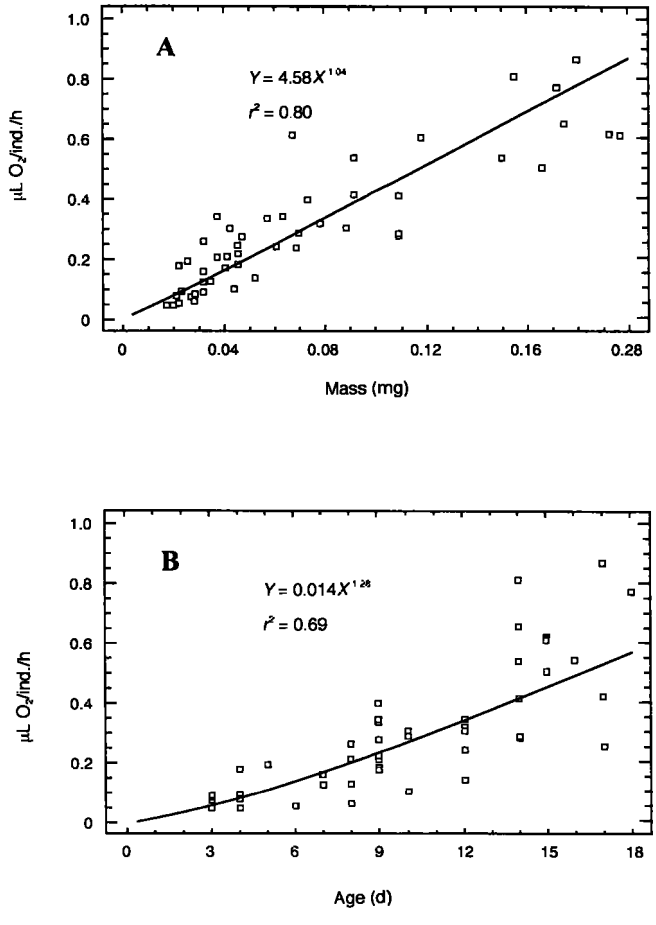

Figure 1

Absolute oxygen consumption (μL O_2/ind./h) in red drum, *Sciaenops ocellatus*, larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

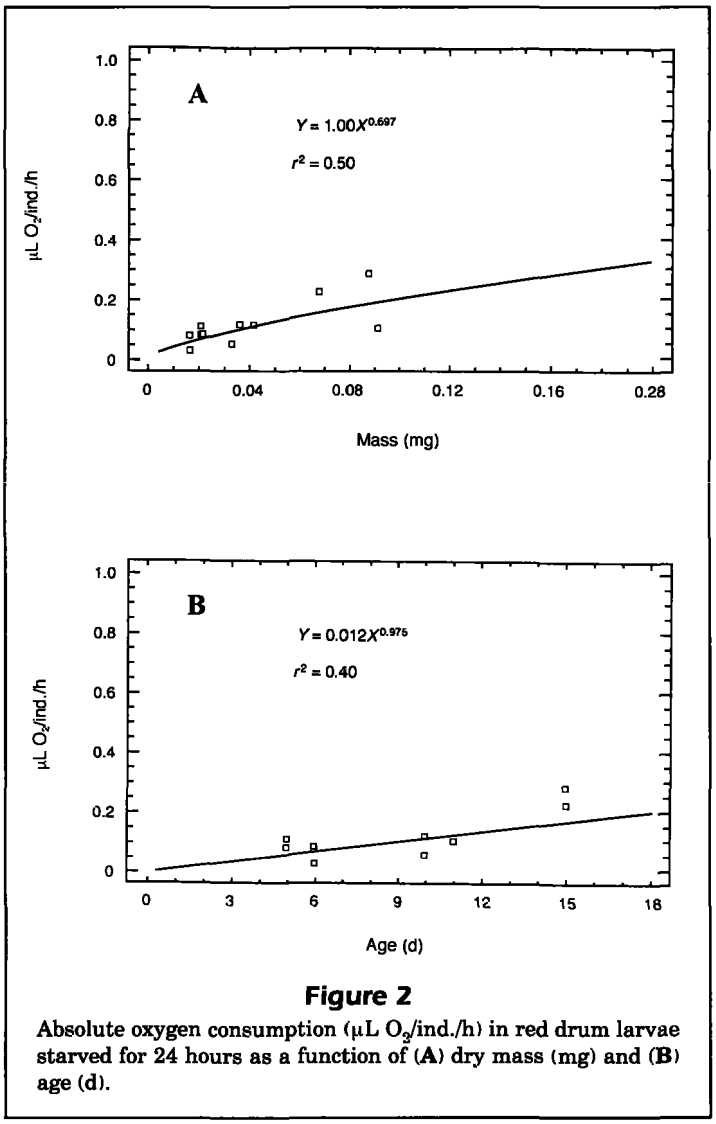

Figure 2

Absolute oxygen consumption (µL O_2/ind./h) in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

had lower O:N ratios than fed larvae on days 6 and 10. Starved larvae had O:NH_3 ratios between 4.3 and 12.0 and O:N ratios between 1.7 and 9.0.

Discussion

Oxygen consumption rates

Absolute oxygen consumption of red drum larvae was similar to that reported for other larval fishes. Fyhn and Serigstag (1987) found absolute oxygen consumption rates of 0.05–0.100 µL O_2/ind./h in cod larvae for the first 5 d of life at 5°C, which, despite the differences in species and temperature, were similar to our results for red drum. A comparison with other subtropical species is offered by the data of Houde (1983) who reported rates of 0.08 to 0.14 µL O_2/ind./h for 25.5 µg-sized sea bream, *Archosargus rhomboidalis*, reared at 26°C, increasing to 0.44–0.62 µL O_2/ind./h in 41–66 µg individuals. Values for red drum

Table 2

Energy allocated to feeding metabolism of red drum larvae during the first two weeks of life. J = joule.

Age (d)	Fed rate (J/ind./h)	Starved rate (J/ind./h)	% reduction
3	0.0015	0.0008	46.7
4	0.0017	0.0010	41.2
6	0.0024	0.0013	45.9
10	0.0044	0.0021	52.2
14	0.0083	0.0033	60.2

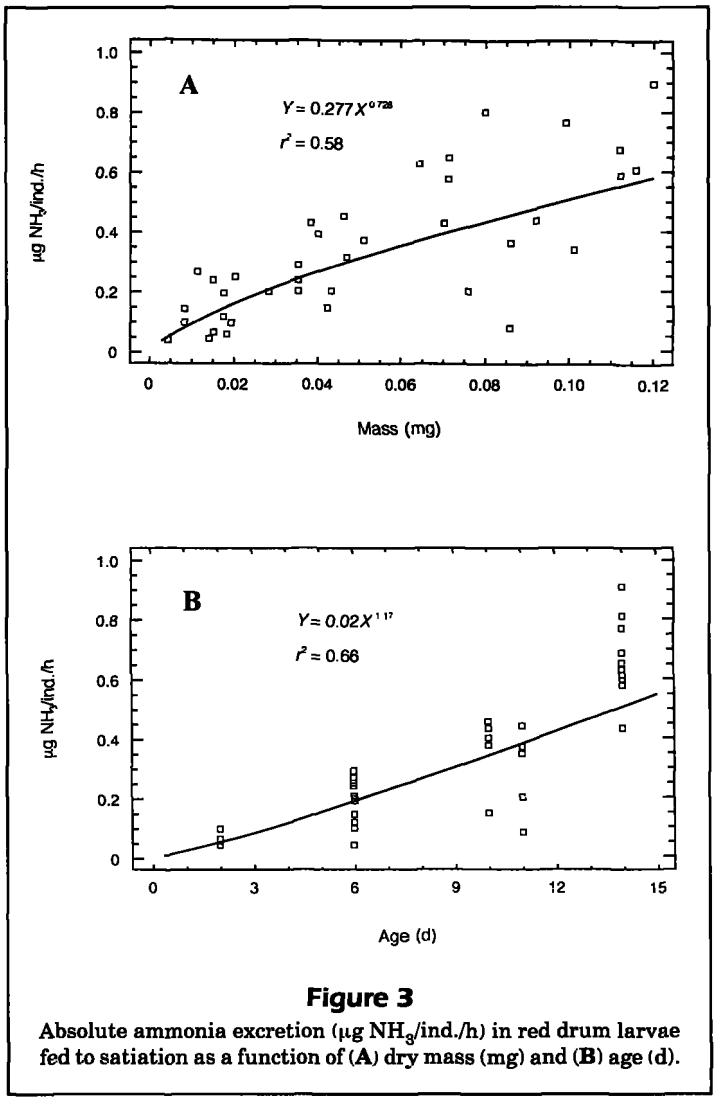

Figure 3

Absolute ammonia excretion (µg NH_3/ind./h) in red drum larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

larvae were lower at 0.05–0.14 µL/ind./h for 21–31 µg fish and 0.26–0.28 µL/ind./h for 52–68 µg larvae.

The regression of absolute oxygen consumption versus mass in larval red drum conformed to the equation $Y = aM^b$ (Fig. 1) and had a slope or "*b* value" of 1.04 (±0.08), which is greater than the most widely used figure of 0.75 (Schmidt-Nielsen, 1983), and the slope of 0.80 commonly cited for adult fish (Brett and Groves, 1979; Houde, 1983; Prasad, 1986). The slope of 1.04 (±0.08) exhibited by red drum larvae indicates that oxygen consumption scaled directly with body mass (1.0) rather than with surface area (0.67). It is becoming increasingly apparent that metabolism scales isometrically with mass in larval fishes (see review by Giguere et al., 1988); thus, a *b* value of 1.0 is the norm rather than the exception for larval fishes and most likely for larval forms in general (Manahan, 1990).

Feeding metabolism

Oxygen consumption rates for two-week-old red drum starved for 24 h declined to about 50% of those for fed individuals (Table 2), which is within the range reported in larval starvation studies with several other species (Holliday et al., 1964; Giguere et al., 1988; Tucker, 1989). The reduction of oxygen consumption in starved versus fed individuals reflects the decrease in energy expenditure associated with feeding metabolism, otherwise known as specific dynamic action (SDA) (Kleiber, 1961; Kiørboe et al., 1985; 1987; Kiørboe, 1989). Jobling (1981a, 1983) suggested that SDA represents the energy expenditure associated with growth. His arguments may be summarized as follows. Biosynthesis is an energy-requiring process (Lehninger, 1985). As a consequence, some fraction of the adenosine triphosphate

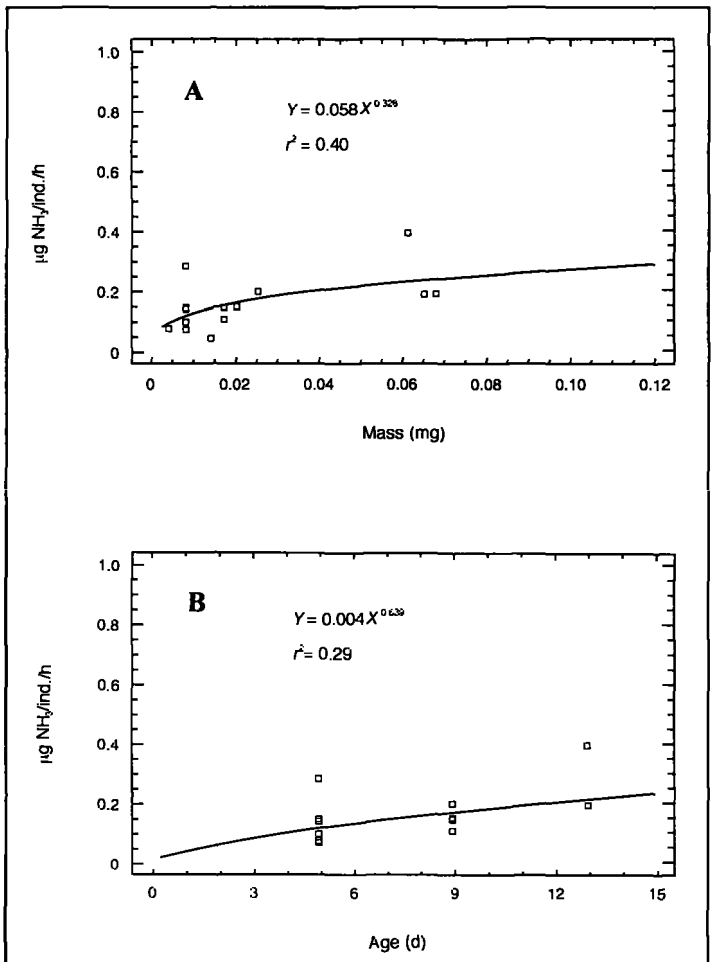

Figure 4

Absolute ammonia excretion in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

(ATP) generated by aerobic metabolism must be used for growth in a normal, developing individual. The fraction of aerobic metabolism that generates the ATP for biosynthesis is the increase in metabolism following feeding variously known as specific dynamic action (SDA) (Kleiber, 1961), specific dynamic effect (Kleiber, 1967), or heat increment (Brett and Groves, 1979). Thus, diets that promote high growth induce high energy use as SDA. Jobling's view conflicts with the more traditional idea that growth and SDA are in direct competition for ingested energy.

The 40% to 60% reduction in metabolic rates of starved individuals indicates that feeding metabolism (SDA) is a substantial fraction of the daily metabolic costs above maintenance in fed larvae. Because SDA is specifically related to growth, and individuals growing slowly demonstrate little change in metabolic rate following feeding (Jobling, 1985), it follows that the large reduction in metabolic rate of starved red drum is indicative of a rapidly growing fish.

Nitrogen excretion

Our data on nitrogen excretion are the first reported for larval red drum; they add significantly to the very limited information describing excretion in fish larvae. Absolute ammonia excretion rates of red drum larvae (Table 3; Fig. 3) were similar to those reported by Klumpp and von Westernhagen (1986) for similar size *Pleuronectes platessa* (0.025–0.050 µg NH_3/ind./h at 100 µg and 11 d) and *Blennius pavo* (0.05–0.10 µg NH_3/ind./h at 100 µg and 5 d).

The 50% drop in absolute and mass-specific ammonia excretion with starvation (Table 3; Figs 3 and 4) mirrors the drop observed in oxygen consumption rate, indicating a general slow-down in metabolic

Table 3

Mean ammonia and urea excretion in red drum larvae fed to satiation and starved for 24 h. n = the number of samples (10 fish per sample); * = 24 h starved; ( ) = standard deviation.

Age (d)	n	Ammonia		Urea	
		µg/ind./h	µm/ind./h ($\times 10^{-3}$)	µm/ind./h ($\times 10^{-3}$)	Excretion % urea
2	5	0.006 (0.001)	0.325 (0.20)	0.0793 (0.08)	32.8
6	10	0.023 (0.007)	1.333 (0.38)	0.2058 (0.03)	23.6
6*	10	0.016 (0.008)	0.660 (0.20)	0.4648 (0.11)	58.5
10	10	0.038 (0.012)	2.215 (0.40)	0.3038 (0.03)	21.5
10*	5	0.015 (0.004)	0.883 (0.23)	0.6678 (0.85)	60.2
14	10	0.067 (0.013)	3.918 (0.78)	0.4205 (0.04)	17.7
14*	5	0.039 (0.001)	2.265 (0.07)	0.4160 (0.25)	32.7

Table 4

Molar oxygen:nitrogen ratios for red drum larvae fed to satiation, and those starved for 24 and 48 h. ( ) = Standard deviation; * = starved 24 hours.

Age (d)	Oxygen (µm/mg/h)	Ammonia (µm/mg/h)	Urea (µm/mg/h)	O:NH_3	O:N
2	0.244 (0.021)	0.024 (0.005)	0.006 (0.005)	10.16 (2.44)	6.78 (1.49)
6	0.367 (0.183)	0.084 (0.039)	0.013 (0.002)	4.37 (3.12)	3.37 (3.02)
6*	0.401 (0.087)	0.089 (0.039)	0.063 (0.014)	4.51 (1.74)	1.86 (0.63)
10	0.598 (0.183)	0.050 (0.018)	0.006 (0.001)	11.96 (2.07)	9.65 (1.70)
10*	0.189 (0.062)	0.044 (0.006)	0.033 (0.004)	4.30 (0.58)	1.72 (0.26)
14	0.321 (0.091)	0.049 (0.008)	0.005 (0.001)	6.55 (1.64)	5.44 (1.37)
14*	0.288 (0.005)	0.024 (0.012)	0.004 (0.003)	12.00 (0.18)	9.00 (0.12)

processes with starvation. As was demonstrated by the O:N ratios (see below), the normally fast-growing young larvae apparently combust their own tissues to fuel their metabolic needs.

Values obtained in the present study for the percentage of nitrogenous waste in the form of urea agree well with previously reported values. Jobling (1981b) found that 15% to 25% of nitrogenous waste in plaice larvae occurred in the form of urea: his values agree well with our values of 18% to 33%. Ammonia as a percent of the total nitrogen excretion increased with age in red drum larvae fed to satiation.

Production of urea may play a role in survival of young larvae. Griffin (1991) proposed that urea synthesis was a mechanism for detoxifying ammonia during early embryogenesis, particularly before hatching, and several investigators have reported the presence of urea-cycle enzymes in larval fish (Rice and Stokes, 1974; Dépêche et al., 1979; Anderson, 1995). Urea costs more energy to produce than ammonia, but it is less toxic. It is used extensively in osmoregulation by elasmobranchs (Anderson, 1995), as an excretory product to prevent poisoning during estivation by African lungfish (Janssens, 1964), and in response to elevated external ammonia levels or to stress in toadfish (Walsh et al., 1990). It is possible that production and retention of urea in young red drum larvae could be used to increase blood osmolarity, in a manner similar to that of elasmobrachs, to aid in osmoregulation. Alternatively, it may be a response to the stress of starvation.

The percent increase in urea production with starvation has been observed in other fishes under hatchery conditions (Brett and Zala, 1975). The constant mass-specific nitrogen excretion in starved fish, despite the changes in relative contributions of ammonia and urea, is indicative of continued protein catabolism. However, the protein catabolized in starved individuals was the protein contained within the larva's own tissues.

Urea normally contributes less than 50% of the total nitrogen excreted and is often overlooked, but the results here suggest urea is an excellent indicator of starvation in larval fishes. The decrease in

percentage of urea excreted by larger red drum larvae could indicate a metabolic shift away from urea production in larvae approaching transformation or in the secondary loss of the ability to produce it (cf. Anderson, 1995).

O:N ratios

Nitrogen excretion data for larval red drum suggest that protein was the major catabolic substrate, with little, if any, energy being stored in, or produced from, lipid reserves. Low O:N ratios in well-fed red drum larvae as well as in those starved for 24 h indicated a protein fuel source in all cases. Ingested rotifers were protein-rich (Brightman, 1993) which almost certainly contributed to the low O:N ratios of fed individuals. The slightly lower O:N ratios for starved larvae suggest an even stronger dependence on protein for metabolic fuel, combusted at the expense of tissue protein.

Conclusions

An interesting outgrowth of the present study is not only the amplitude of change in metabolism with starvation, but the change in the scaling coefficient as well. The drop in "*b*" from 1.04 to 0.697 as a result of starvation suggests that the larger larvae have sustained a proportionately greater drop in metabolism than the smaller ones, which, in turn, underscores a metabolic "catch-22" situation in young larvae. Rapid growth of a larva decreases the number of its potential predators, thereby giving the larva the ecological refuge of increased size. In addition, it simultaneously increases the size range of its potential prey. However, the fact that metabolism scales directly with mass means that larger larvae will also be combusting more metabolic fuel in an absolute sense than will smaller individuals. Because energy storage in red drum larvae is almost nonexistent (Brightman, 1993), the absolute metabolic costs of being larger could prove to be rapidly debilitating during times of starvation (cf. Giguere, 1988). In juvenile and adult fishes, "*b*" values typically are close to 0.80 (Giguere, 1988) and weight-specific oxygen consumption declines with increasing size. Thus, in adult fish, larger size gives a metabolic refugium as well as an ecological one. Because larger adults have a proportionately lower metabolism than smaller adults, starvation will be proportionately less debilitating for the larger fish. Thus, the "catch-22" of isometric scaling (b=1.0) in the very early life history of fish is that it is almost certainly part of the metabolic underpinnings of rapid growth, but it also makes larger larvae nearly as vulnerable to starvation as smaller ones. Rapid growth gives an ecological refuge but it comes at the expense of physiological vulnerability.

Acknowledgments

The authors would like to thank Bill Falls, Anne Burke, and Dan Roberts of the Florida Department of Environmental Protection's Marine Research Institute for providing red drum eggs and for their considerable help in teaching us culture techniques. This research was supported by FDEP contract C-7701 and NSF OCE 92-18505 to J. J. Torres.

Literature cited

Anderson, P. M.
1995. Urea cycle in fish: molecular and mitochondrial studies. *In* C. M. Wood and T. J. Shuttleworth (eds.), Fish physiology, vol. 14: Cellular and molecular approaches to fish ionic regulation, p. 57–83. Academic Press, London.

Bayne, B. L.
1973. Physiological changes in *Mytilus edules L.* induced by temperature and nutritive stress. J. Mar. Biol. Assoc. U.K. 53:39–58.

Blaxter, J. H. S.
1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115:98–114.

Brett, J. R., and T. D. D. Groves.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R.. Brett (eds.), Fish physiology, vol. VIII: Bioenergetics and growth, p. 279–351. Academic Press, New York, NY.

Brett, J. R., and C. A. Zala.
1975. Daily patterns of nitrogen excretion and oxygen consumption of fingerling sockeye salmon, *Oncorhynchus nerka,* under controlled conditions. J. Fish. Res. Board Can. 26:2363.

Brightman, R. I.
1993. Energetics and RNA/DNA of red drum larvae *Sciaenops ocellatus*. Ph.D. diss., Univ. South Florida, 178 p.

Davenport, J., S. Lonning, and E. Kjorsvik.
1983. Ammonia output by eggs and larvae of the lumpsucker, *Cyclopterus lumpus*, the cod, *Gadus morhua* and the plaice, *Pleuronectes platessa*. J. Mar. Biol. Assoc. U.K. 63:713–723.

Dépêche, J., R. Giles, S. Daufresne, and H. Chiapello.
1979. Urea content and urea production via the orinithine-urea cycle pathway during the ontogenic development of two teleost fishes. Comp. Biochem. Physiol. 63:51–56.

de Silva, C.
1974. Development of the respiratory system in herring and plaice larvae. *In* J. H. S. Blaxter (ed.), Early life history of fish, p. 465–485. Springer-Verlag, New York, NY.

Donnelly, J., and J. J. Torres.
1988. Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. Mar. Biol. 97:483–494.

Fyhn, H. J., and B. Serigstad.
1987. Free amino acids as energy substrate in developing

eggs and larvae of the cod *Gadus morhua*. Mar. Biol. 96:335–341.

Griffith, R. W.
1991. Guppies, toadfish, lungfish, coelacanths and frogs: a scenario for the evolution of urea retention in fishes. Environ. Biol. Fishes 32:199–218.

Giguere, L. A., B. Cofe, and J. F. St.-Pierre.
1988. Metabolic rates scale isometrically in larval fishes. Mar. Ecol. Prog. Ser. 50:13–19.

Hoff, F. H., and T. W. Snell.
1987. Plankton culture manual. Florida Aqua Farms, Dade City, Florida, 98 p .

Holliday, F. G. T., J. H. S. Blaxter, and R. Lasker.
1964. Oxygen uptake of developing eggs and larvae of the herring *(Clupea harengus)*. J. Mar. Biol. Assoc. U.K. 44:711–723.

Houde, E. D.
1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical marine fishes. Mar. Biol. 72:283–293.
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–495.

Janssens, P. A.
1964. The metabolism of the aestivating African lungfish. Comp. Biochem. Physiol. 11:105–117.

Jobling, M.
1981a. Some effects of temperature, feeding and body weight on nitrogenous excretion in young plaice *Pleuronectes platessa*. J. Fish Biol. 18:87–96.
1981b. The influences of feeding on the metabolic rate of fishes: a short review. J. Fish Biol. 18:385.
1983. Towards an explanation of specific dynamic action (SDA). J. Fish Biol. 21:357.
1985. Growth. *In* P. Tytler and P. Calow (eds.), Fish energetics: new perspectives, p. 213–230. Croom Helm, London.

Kiorbøe, T.
1989. Growth in fish larvae: Are they particularly efficient? Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:383–389.

Kiorbøe, T., F. Mohlenberg, and K. Hamburger.
1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration and composition of specific dynamic action. Mar. Ecol. Prog. Ser. 26:85–97.

Kiorbøe, T., P. Munk, and K. Richardson.
1987. Respiration and growth of larval herring *Clupea harengus*: relation between specific dynamic action and growth efficiency. Mar. Ecol. Prog. Ser. 40:1–10.

Kleiber, M.
1961. The fire of life: an introduction to animal energetics. John Wiley and Sons, Inc. New York, NY, p. 454.
1967. The fire of life: an introduction to animal energetics, second ed. John Wiley and Sons, Inc. New York, NY, p. 454.

Klumpp, D. W., and H. von Westernhagen.
1986. Nitrogen balance in marine fish larvae: influence of developmental stage and prey density. Mar. Biol. 93: 189–190.

Lehninger, A. L.
1985. Principles of biochemistry. Worth Publishers, New York, NY, 1011p.

Manahan, D. T.
1990. Adaptations by invertebrate larvae for nutrient acquistion from seawater. Am. Zool. 30:147–160.

Mickel, T. J., L. B. Quetin, and J. J. Childress.
1983. Construction of a polarographic oxygen sensor in the laboratory. *In* E. Gnaiger and H. Forstner (eds.), Polarographic oxygen sensors: aquatic and physiological applications, p. 81–85. Springer-Verlag, New York, NY.

Prasad, M. S.
1986. Oxygen uptake during early life in the fresh water fish, *Esomus danricus* (Ham) (Pisces, Cypriniformes). Acia Physiologica Hungarica. 67:367–376.

Pennycuick, C. J.
1988. Conversionfactors: SI units and many others. Univ. Chicago Press, Chicago and London, p. 36.

Price, N. M., and P. J. Harrison.
1987. Comparison of the methods for the analysis of dissolved urea in seawater. Mar. Biol. 94:307–317.

Revsbech, N. P., and D. M. Ward.
1983. Oxygen microelectrode that is insensitive to medium chemical composition: use in an acid microbial mat dominated by *Cyanidium caldarium*. Appl. Environ. Microbiol. 45:755–759.

Rice, S. D., and R. M. Stokes.
1974. Metabolism of nitrogenous wastes in the eggs and alevins of the rainbow trout, *Salmo gairdneri* Richardson. *In*. J.H.S. Baxter (ed), The early life history of fish, p. 325–337. Springer-Verlag, New York, NY.

Roberts, D. E. Jr., L. A. Morey, G. E. Henderson, and K. Halscott.
1978. The effects of delayed feeding, stocking density, and food density on survival, growth, and production of larval red drum. Proc. 9th annual meeting of the World Mar. Soc., Atlanta, Georgia; 3–6 Jan 1978. p. 333–343.

Schmidt-Nielson, K.
1983. Animal physiology: adaptation and environment. Cambridge Univ. Press, New York, NY, 619 p.

Tucker, J. W. Jr.
1989. Energy utilization in bay anchovy, *Anchoa mitchilli*, and black sea bass, *Centropristis striata*, eggs and larvae. Fish. Bull. 78:279–293.

Walsh, P. J., E. Danulat, and T. P. Mommsen.
1990. Variation in urea excretion in the gulf toadfish *(Opsanus beta)*. Mar. Biol. 106:323–328.

Weatherly, A. H., and H. S. Gill.
1987. The biology of fish growth. Academic Press, New York, NY, 443 p.

Weihs, D.
1981. Swimming of yolk-sac larval anchovy *(Engraulis mordax)* as a respiration mechanism. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:327.