

Energetics of swimming in juvenile common snook, *Centropomus undecimalis*

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Synopsis

Little research has been devoted to the investigation of swimming energetics and performance in lie-in-wait predators. This study evaluated activity metabolism and swimming performance in juvenile snook, *Centropomus undecimalis*, a lie-in-wait predator, by determining oxygen uptake in a tunnel respirometer. Compared to previously reported results for more actively foraging species (i.e., white crappie, rainbow trout), snook exhibited lower maintenance metabolism (58.6 ml O₂ kg⁻¹ WM h⁻¹) and greater metabolic expansibility (6.5). Relative critical swimming speeds decreased isometrically with length, implying that small snook are capable of prolonged swimming in velocity regimes similar to those experienced by larger individuals. Swimming was most efficient at the transition between pectoral (low-speed) and caudal (high-speed) propulsion. The results of this study support previous speculation that maintenance costs may be reduced in lie-in-wait predators compared to other fishes.

Introduction

The analysis of oxygen uptake and swimming performance provides insight into the interaction between metabolic supply and demand in fishes. Because both oxygen uptake and performance respond to a variety of intrinsic and environmental factors (Fry 1971), they have been consistently relied upon as criteria of organism health. Body form and size influence thrust production and hydrodynamic drag (Webb 1978); increased size also results in reduced mass-specific metabolism reflecting changes in the transport mechanics for materials essential to metabolic processes (West et al. 1997). Sex and reproductive state also have been identified as operative internal factors (Facey & Grossman 1990, Adams & Parsons 1998). Important extrinsic considerations include temperature (Rome et al. 1985, Johnston et al. 1991), salinity (Nordlie et al. 1991, Abud 1992), oxygen tension

(Subrahmanyam 1980, Parsons & Carlson 1998), diet (Beamish et al. 1989), and photoperiod (Kolok 1991).

Because any gain in swimming efficiency has the potential to improve fitness, natural selection would be expected to shape the interaction between metabolic supply and demand (Priede 1985). Models have been developed that predict optimal swimming speeds in fishes (Weihs 1977, Ware 1978, Wakeman & Wohlschlag 1982) and cost of transport analysis has been used to identify these velocities (Bernatchez & Dodson 1985, Parsons & Sylvester 1992).

Nevertheless, the characterization of energy partitioning and swimming efficiency can be problematic for some fishes. Even in the otherwise well studied northern pike, *Esox lucius*, the determination of activity metabolism has proven difficult. A lie-in-wait predator, this species will not swim steadily against a current (Armstrong 1986) and may even damage itself struggling against the confines of a tunnel respirometer

(Priede & Tytler 1977), making it less amenable to the use of standardized techniques that assess metabolic costs and swimming performance.

Like the northern pike, the common snook, *Centropomus undecimalis*, is a lie-in-wait predator (sensu Moyle & Cech 2000). This largely tropical species (Rivas 1986) is a highly prized gamefish in Florida, where considerable effort has been expended toward its culture. Unlike pike, snook consistently exhibit positive rheotaxis and perform well in a swim tunnel. In this study, activity-specific metabolism and swimming performance of common snook were assessed using a tunnel respirometer.

Material and methods

Collection and feeding

Juvenile snook were collected using 6.4-mm mesh seines at various locations on the Little Manatee River, a tributary of Tampa Bay, Florida. Fish were maintained in 560 l fiberglass aquaria equipped with biological filters and were gradually weaned from a diet of live fish to a commercially prepared one (3.2 mm soft-moist salmon pellets). Fish were fed until satiated; frequency of feeding was every other day. All fish had been feeding on the prepared diet for a minimum of four months prior to the experiments.

Respirometry

The Brett-type tunnel respirometer employed (40 l) was modified from a design proposed by Bell & Terhune (1970). Flow was regulated using a centrifugal pump and motor assembly that allowed for variable speed control. Flow velocity was calibrated using a paddle-wheel sensor and analog flow meter. Because the cross-sectional areas of juvenile snook tested were less than 10% that of the chamber, no corrections for solid blocking effects were necessary (Smit et al. 1971). Temperature was maintained at $23 \pm 1^\circ\text{C}$ using a heat exchanger coupled to a recirculator unit; salinity mirrored that in the holding aquaria (12‰) and approximated isosmotic conditions in order to minimize metabolic costs associated with osmoregulation (Pérez-Pinzón & Lutz 1991).

Oxygen concentration was monitored continuously using a polarographic electrode coupled to an amplifier and a chart recorder. The electrode was calibrated

using nitrogen- and air-equilibrated water and was recalibrated between trials. Oxygen uptake (V_{O_2}), expressed as $\text{ml O}_2 \text{ kg}^{-1} \text{ wet mass (WM) h}^{-1}$, was estimated using the slope of the relationship between O_2 concentration and time; blanks were run at each velocity to account for O_2 uptake of the respirometer itself. Oxygen tension within the chamber was maintained at 60–100% of saturation values.

Fasting (24 h) reduced defecation within the respirometer and ensured a post-absorptive state, thereby minimizing additional oxygen uptake due to apparent heat increment (Duthie & Houlihan 1982). In order to reduce the effects of handling on swimming performance, animals were allowed to recover in the respirometer for a minimum of 2 h prior to each experiment (Glova & McInerney 1977, Kolok 1991). Fish were shielded from the external environment but were provided with visual cues inside the chamber to facilitate station holding during swimming.

Swimming protocol

Oxygen concentration was monitored during prescribed bouts of 30 min (Farlinger & Beamish 1977). With each subsequent bout, velocity was increased by 5 cm s^{-1} ; between bouts, fish were allowed to rest for 15 min (Baltz et al. 1982, Parsons & Sylvester 1992, Adams & Parsons 1998) at a velocity of approximately 2 cm s^{-1} . Successive bouts were carried out until, after repeated efforts, fish could no longer hold themselves off the retention screen at the rear of the chamber. At this stage, fish were considered fatigued, and the trials were terminated. Individuals were removed from the respirometer, anesthetized with tricaine methanesulfonate, measured to the nearest 1 mm standard length (SL), and weighed to the nearest 0.1 g wet mass (WM). No fish was used more than once.

Standard (maintenance) metabolic rate was estimated using the y-intercept of the relationship between V_{O_2} and swimming speed for all individuals tested. Critical swimming speeds sensu Brett (1964) were calculated using the fatigue time from each trial. Caudal and pectoral fin beat frequencies were estimated for each fish at each swimming speed as the observed number of fin beats recorded during a 5-sec time period. Cost of transport was estimated as the mass-specific metabolic cost associated with swimming a given distance (Schmidt-Nielsen 1972) and was compared to swimming speed in order to examine swimming efficiency.

Results

Oxygen uptake

Oxygen uptake in juvenile snook (138–200 mm SL; 36.4–112.2 g WM) exhibited significant variation with respect to swimming speed (ANOVA, $F = 23.94$, $df = 79$, $p < 0.0001$). Although respiration rates calculated for swimming speeds of 5–25 cm s^{-1} did not vary (least significant difference), these values were significantly lower than rates calculated for swimming speeds of 30 cm s^{-1} and above. The relationship between oxygen uptake and swimming velocity was described using an exponential model (Brett 1964, Webb 1975), which explained 56% of the variation in the data: $V_{\text{O}_2} = e^{(4.06+3.99 \cdot 10^{-2} \cdot u)}$, where V_{O_2} is mass-specific oxygen consumption ($\text{ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$) and u is absolute swimming speed (cm s^{-1}). In order to account for size-specific variation in respiration, oxygen uptake also was regressed on relative swimming speed (u_r) expressed as body lengths (bl s^{-1}). The resulting model, $V_{\text{O}_2} = e^{(4.07+6.44 \cdot 10^{-1} \cdot u_r)}$, provided a slightly improved fit to the data (Figure 1). Standard metabolic rate was calculated at 58.6 $\text{ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ using this relationship. Active metabolic rate, the oxygen uptake determined at the critical swimming speed, averaged $380.1 \pm 74.7 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$; metabolic expansibility, the ratio of active:standard metabolic rates (Robinson et al. 1983) was therefore 6.5.

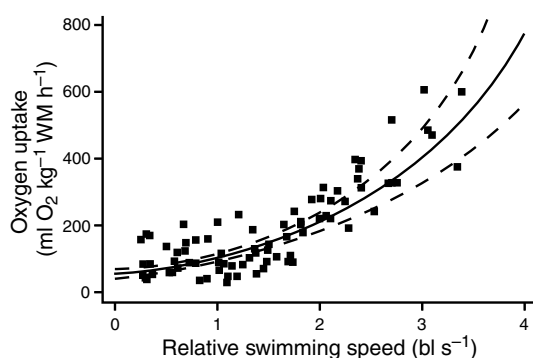


Figure 1. Oxygen uptake of juvenile snook as a function of relative swimming velocity: $V_{\text{O}_2} = e^{(4.07+6.44 \cdot 10^{-1} \cdot u_r)}$, where V_{O_2} is oxygen uptake expressed as $\text{ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ and u_r is relative swimming speed in bl s^{-1} ($r^2 = 0.60$; $n = 80$; $p < 0.00001$). Standard metabolic rate, estimated at zero swimming speed, is 58.6 $\text{ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$. Dashed lines represent 95% confidence limits.

Swimming performance

Critical swimming speeds in snook ranging in size from 47 to 212 mm SL varied from 41.4 to 57.2 cm s^{-1} corresponding to 2.2–8.9 bl s^{-1} . Although absolute critical swimming speed (cm s^{-1}) was not correlated with fish size, relative critical swimming speed (bl s^{-1}) decreased significantly with length ($r^2 = 0.97$, $df = 15$, $p < 0.00001$): $U_{\text{crit}} = 3.79 \cdot 10^2 \cdot \text{SL}^{-0.96}$ (Figure 2).

The use of caudal and pectoral fins diverged with increasing velocity (Figure 3). Caudal fin movement was positively correlated with swimming speed ($r = 0.91$, $df = 89$, $p < 0.00001$); pectoral fin beat frequency differed significantly between low (5–20 cm s^{-1}) and high (25–60 cm s^{-1}) velocities (ANOVA, $F = 20.99$, $df = 85$, $p < 0.0001$, least significant difference).

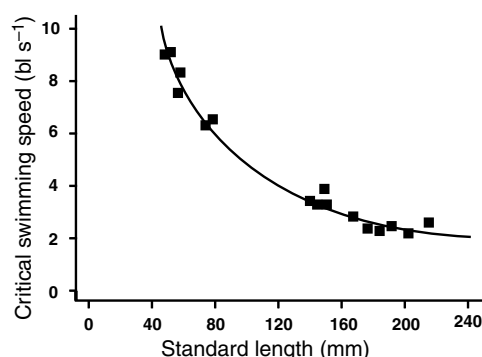


Figure 2. Effect of fish size on relative critical swimming speed (bl s^{-1}) ($r^2 = 0.97$; $n = 16$; $p < 0.00001$).

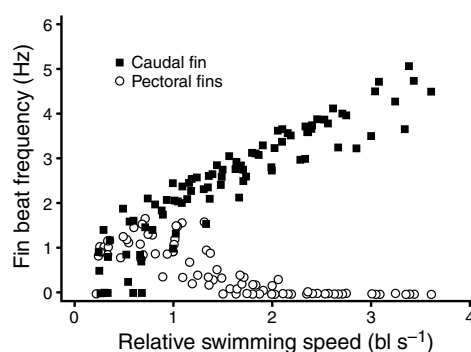


Figure 3. Relative contributions of caudal and pectoral fin movement to the production of thrust at different swimming velocities. Each point represents the average of five observations (caudal fin, $n = 92$; pectoral fins, $n = 85$).

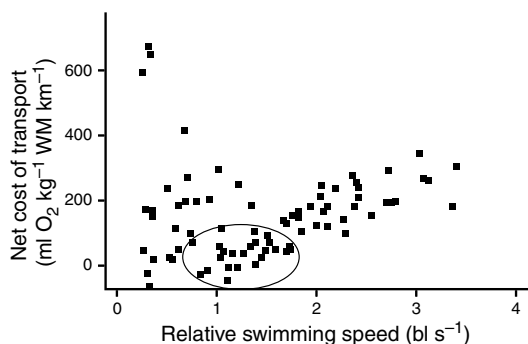


Figure 4. Net cost of transport as a function of relative swimming velocity. The concentration of reduced transport costs identified by the ellipse suggests that optimal swimming occurs at velocities slightly above 1 bl s^{-1} .

Both total and net (that exclusive of standard metabolism) costs of transport exhibited significant variation among swimming speeds (Kruskal–Wallis test, $w = 38.33$, $p < 0.0001$ and $w = 20.43$, $p = 0.015$, respectively). With increasing speed, median total cost of transport first decreased to values of 117.8 and $119.0 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM km}^{-1}$ at 20 and 25 cm s^{-1} before increasing at higher velocities. Minimum values calculated for swimming speeds of 20 and 25 cm s^{-1} , corresponding to 1.2 – 1.5 bl s^{-1} , were significantly lower than those calculated for speeds of 10 cm s^{-1} or less and for speeds of 35 – 45 cm s^{-1} (notched box-and-whisker plot, 95% confidence intervals). Net cost of transport exhibited a similar trend with minimum median values of 36.4 and $53.9 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM km}^{-1}$ occurring at 20 and 25 cm s^{-1} respectively. These values were significantly lower than those calculated for swimming speeds of 35 cm s^{-1} and above (notched box-and-whisker plot, 95% confidence interval). An examination of the relationship between net cost of transport and relative swimming speed also suggests that optimal swimming in juvenile snook occurs at velocities slightly greater than 1 bl s^{-1} (Figure 4).

Discussion

Due to the difficulties inherent in applying standard techniques of respirometry to fish such as northern pike, little research has been devoted to the investigation of swimming energetics and performance in lie-in-wait predators. Lucas et al. (1991) have had some success in addressing this problem by using heart-rate telemetry in wild fish, but this technique too has its limitations

(see Priede & Tytler 1977, Armstrong 1986). The current study analyzed activity-specific oxygen uptake in juvenile snook in order to estimate the costs of both maintenance and activity metabolism in a lie-in-wait predator. This study also identified scaling effects and optimal swimming speeds by examining swimming performance.

The lack of variation in oxygen uptake at swimming speeds below 25 cm s^{-1} suggests that maintaining position within the respirometer did not constitute a significant energy demand at these velocities and that oxygen uptake more likely tracked routine activity. Mean oxygen uptake measured at these speeds (100.6 – $125.2 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$) was similar to routine rates reported for other estuarine fishes occurring sympatrically with snook in southwest Florida: spotted seatrout, *Cynoscion nebulosus*, and sand seatrout, *Cynoscion arenarius*, 86 and $120 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ at 30°C (Vetter 1982); spot, *Leiostomus xanthurus*, and pinfish, *Lagodon rhomboides*, 85 – $112 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ and 76 – $96 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ (Subrahmanyam 1980).

Standard metabolic rate estimated here ($58.6 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$) agreed well with rates calculated for young snook by Pérez-Pinzón & Lutz (1991) for fresh water and seawater (55.98 and $55.21 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$ respectively); however, it was considerably higher than that reported by these authors for similar isosmotic conditions ($33.94 \text{ ml O}_2 \text{ kg}^{-1} \text{ WM h}^{-1}$). Pérez-Pinzón & Lutz (1991) argued that differences in standard metabolism between isosmotic and either freshwater or seawater conditions could be accounted for by reduced osmoregulatory costs. Because osmoregulatory capability in fishes can vary with ontogeny (e.g., Kreeger 1995), this discrepancy may reflect between-study differences in fish size: 36.4 – 112.2 g , this study; 1.5 – 2.0 g (Pérez-Pinzón & Lutz 1991). Moreover, although the 2-h acclimation period used in the current study may have been adequate to minimize the influence of pretest handling on swimming performance, this interval may not have been sufficient to insulate oxygen uptake from similar sources of stress. In his review, Beamish (1978) noted that fish were usually allowed to recover from handling effects for 12 – 16 h prior to testing. Therefore, oxygen uptake reported here might have been elevated due to insufficient acclimation. This influence, if present, would have been most pronounced earlier in the trials, while fish were swimming at reduced velocities, and could have resulted in an overestimation of standard metabolic rate.

Johnson (1966) calculated high food conversion efficiency in the northern pike, and speculated that this was a consequence of the lower maintenance requirements of lie-in-wait predators. In order to address this question, Wieser & Medgyesy (1991) constructed and compared energy budgets for juvenile northern pike and perch, *Perca fluviatilis*, a more actively foraging predator. Although these authors found similar patterns of energy utilization between the two species, they did not estimate standard metabolic rate and therefore did not specifically address the issue of maintenance metabolism.

To revisit this question, we compared metabolic results for juvenile snook with similar results determined for more actively foraging species—white crappie, *Pomoxis annularis*, a deep-bodied fish (sensu Moyle & Cech 2000), and rainbow trout, *Oncorhynchus mykiss*, a rover predator (sensu Moyle & Cech 2000). These species were selected for comparison because the size range of individuals tested overlapped that of juvenile snook in the present study and because metabolic data were collected at similar temperatures: white crappie, 165–175 mm SL, 89–96 g WM, 25°C (Parsons & Sylvester 1992); rainbow trout, 185 ± 20 mm SL, 52.2 ± 20.2 g WM, 24°C (Brett 1964). Standard metabolic rate in young snook, 83.7 mg O₂ kg⁻¹ WM h⁻¹ (58.6 ml O₂ kg⁻¹ WM h⁻¹) was lower than that reported for either white crappie (121.5 mg O₂ kg⁻¹ WM h⁻¹) (Parsons & Sylvester 1992) or rainbow trout (196.5 mg O₂ kg⁻¹ WM h⁻¹) (Brett 1964). Moreover, metabolic expansibility in snook (6.5) was much higher than values estimated using the metabolic data from white crappie and rainbow trout (2.7 and 4.3, respectively). These results support the notion that maintenance costs in lie-in-wait predators may be reduced compared to other fishes, resulting in greater metabolic expansibility.

When standardized to fish length, critical swimming speeds decreased isometrically with size. Such a reduction in relative performance was predicted by Beamish (1978) on theoretical grounds and has been demonstrated previously (Turnpenny & Bamber 1983, Moffat & Davison 1986); it implies that small juveniles are capable of prolonged swimming in the same velocity regimes as larger juveniles. Wakeman & Wohlschlag (1982) maintained that least-cost swimming in pelagic estuarine fishes followed a similar trend with smaller individuals cruising optimally at higher relative velocities (bl s⁻¹) compared with larger fish.

The relative contributions of caudal and pectoral fins to the development of thrust diverged with increasing

velocity: although caudal fin use increased with velocity, pectoral fins were used primarily at lower speeds (10–15 cm s⁻¹) and were relied upon solely for steering at higher velocities. Parsons & Sylvester (1992) observed similar patterns of pectoral fin use in the white crappie. In contrast to snook, the caudal fin of white crappie was recruited at intermediate speeds and was not used at velocities below 15 cm s⁻¹.

Optimal swimming speeds calculated for juvenile snook ranged from 20 to 25 cm s⁻¹ (1.2–1.5 bl s⁻¹) based on cost of transport analysis, and are in agreement with the theoretical value of 23.2 cm s⁻¹ calculated from Weihs' (1977) model relating optimal swimming and body size. The increase in swimming efficiency of snook occurred at the transition between pectoral (low-speed) and caudal (high-speed) swimming. Swimming efficiency in the white crappie also was highest at the transitional speeds of 20–25 cm s⁻¹ and Parsons & Sylvester (1992) speculated that an energetic advantage was gained by using both fin types to produce thrust. It is more likely that this pattern simply reflects the underlying interplay among transit time, speed of muscle contraction, and drag. At very low swimming velocities, transit time is the prime determinant of energetic cost; however, at higher swimming speeds, the combined effects of increased rate of muscle contraction and the non-linear influence of profile drag predominate.

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