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Variation in routine metabolism of juvenile muskellunge: evidence for seasonal metabolic compensation in fishes

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Metabolic rate of age 0 muskellunge *Esox masquinongy* ranged from 0·10 at 5° C to 0·24 mg O_2 g^{-1} h^{-1} at 25° C and was significantly higher in spring and autumn than during winter months at comparable water temperatures. Reduced metabolic rate in winter was consistent with the metabolic compensation hypothesis, implying that metabolism of muskellunge varies independently of acclimation temperature and gonadogenesis. Moreover, seasonal variation in metabolic rate has important implications for energy budget studies. Single-season estimates of esocid metabolism may be inadequate to describe annual energy requirements: the magnitude of errors will depend on the time of year metabolic rate was measured. As a result, it is suggested that seasonal variation in metabolic rate be incorporated into energy budget determinations for fishes.

Key words: bioenergetics; routine metabolic rate; *Esox masquinongy*; gonadogenesis.

INTRODUCTION

Seasonal variation in metabolic rate of fishes has been described for a variety of taxa (Winberg, 1956; Wohlschlag & Juliano, 1959; Beamish, 1964; Meakins, 1975; Evans, 1984; Adams & Parsons, 1998). Because metabolism can vary independently of acclimation temperature, simple thermokinetic responses may not predict annual respiratory requirements of fish adequately (Winberg, 1956; Evans, 1984). Identifying factors that affect seasonal variation in metabolic rates can have important implications for understanding physiological adaptations in fishes.

Seasonal variation in metabolic rate of fishes has often been attributed to gonadogenesis associated with the spawning period (Beamish, 1964, 1990; Adams & Parsons, 1998). At a given water temperature, metabolic rate of fishes is typically higher during the spawning period than at other times of the year (Beamish, 1964; Adams & Parsons, 1998). Although less frequently studied, seasonal changes in metabolic rate of immature fishes have also been reported (Wohlschlag & Juliano, 1959; Withey & Saunders, 1973). Studies of juvenile Atlantic salmon *Salmo salar* L., for example, demonstrated lower metabolic rate for fish exposed to winter photoperiods (Withey & Saunders, 1973), implying

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that these fish undergo an anticipatory response to seasonal environmental conditions (Fry, 1964; Evans, 1984). The anticipatory response, as described by Fry (1964), is independent of water temperature and changes in a direction that is physiologically compatible with environmental conditions (Evans, 1984). For fishes, reduced metabolic requirements in winter months coincide with reduced food availability and lower activity levels (Evans, 1984). Differentiating effects of gonadogenesis or metabolic compensation is difficult in adult fishes since either or both could affect metabolic rate at the same time. Although gonadogenesis can affect metabolic rate of mature fishes, it may not provide an adequate explanation for seasonal metabolic rhythms in immature fishes. An alternative hypothesis suggests that seasonal metabolic compensation occurs in some fishes, although evidence for this remains scant. Hence, additional studies with juvenile fishes are needed to help strengthen generalizations concerning effects of these two alternative mechanisms on fish metabolism.

In this study, effects of water temperature and time of year were examined on routine metabolic rate of immature muskellunge *Esox masquinongy* Mitchill. It was postulated that metabolic rate of juvenile fish would vary with season, consistent with the anticipatory response hypothesis (Fry, 1964; Evans, 1984). In addition, the implications are discussed of seasonally variable metabolic rate and timing of respiratory experiments on metabolic parameters in fish bioenergetic models.

MATERIALS AND METHODS

FISH SOURCE AND ACCLIMATION

Age-0 muskellunge were obtained from the Minnesota Department of Natural Resources, U.S.A., in July and August 1991 and 1992. Muskellunge were held in the laboratory at 20° C and fed live fathead minnows *Pimephales promelas* Rafinesque daily. Prior to experiments, water temperature in the rearing tanks was adjusted at a rate of *c.* 2° C day^{-1} and fish were maintained at each test temperature for 2 weeks before initiating experiments. Routine metabolic rate was measured at 5, 15, and 25° C in autumn (October–November), winter (January–February) and spring (April–May) periods from 1992 to 1993. To simulate seasonal photoperiod, light level was maintained at 12 h light : 12 h dark in spring and autumn and 10 h light : 14 h dark in winter months.

METABOLIC RATE

Routine metabolic rate of muskellunge was measured using closed-vessel respirometry (Cech, 1990). Experiments were conducted in an environmental chamber to control temperature and photoperiod. Four to eight fish were tested at each water temperature and two to three replicate measurements obtained on each fish. Mean weight of fish used in experiments ranged from 9·6 to 19·2 g (Table I). Fish were sealed in a 2·4-l glass chamber covered by a Plexiglas lid which was fitted with a polarographic dissolved oxygen probe as well as a water inlet and outlet tube (Clapp & Wahl, 1996). The chamber was filled with aerated water and flushed of waste products before and after each experiment. Prior to experiments, fish were starved for 1–3 days depending on gastric evacuation rates (Bevelhimer *et al.*, 1985), and then transferred into test chambers 24 h before tests began. To mix water thoroughly inside the test chamber, a magnetic stirrer was activated for 3 min prior to the beginning and ending of each test. Oxygen concentrations inside the test chamber were output to a computer at 30-s intervals and tests were conducted until adequate oxygen consumption could be measured, which was generally 0·75–1·5 h depending on water temperature (Bevelhimer *et al.*, 1985; Clapp & Wahl, 1996). When fish were active inside the test chamber, water movement around the

Table I. Mean mass and routine metabolic rate (±95% CI) of age 0 muskellunge measured in spring, autumn and winter at 5, 15, and 25° C

Temperature (° C)	Season	n	Mean mass (g)	Routine metabolic rate (mg O_2 g^{-1} h^{-1})
5	Spring	5	19·2 (6·1)^{z}	0·117 (0·016)
	Autumn	6	12·9 (1·6)^{y}	0·104 (0·014)
	Winter	6	12·2 (2·1)^{y}	0·101 (0·016)
15	Spring	4	19·0 (1·5)^{z}	0·189 (0·014)
	Autumn	8	12·2 (1·8)^{y}	0·210 (0·014)
	Winter	5	14·0 (2·8)^{y}	0·147 (0·010)
25	Spring	7	15·9 (2·8)^{z}	0·239 (0·016)
	Autumn	4	11·2 (1·1)^{y}	0·238 (0·030)
	Winter	4	9·6 (3·8)^{y}	0·216 (0·035)

For each temperature, means for fish mass with the same letter are not significantly different (Tukey's multiple comparison test; $P>0{\cdot}05$). Photoperiods were 12 h light : 12 h dark for spring and autumn and 10 h light:14 h dark for winter periods.

oxygen probe caused irregular fluctuations in oxygen concentration. Variation in 30-s measures of oxygen concentration were examined to determine the degree of activity inside the test chamber (Bevelhimer *et al.*, 1985). Most fish (>90%) exhibited little activity during tests. However, trials were excluded where the coefficient of variation associated with oxygen concentration was >15%, which generally corresponded to observations where fish were active >25% of the time.

At the completion of each test, muskellunge were anaesthetized and measured to the nearest 0·1 g. Oxygen consumption (O; mg O_2 h^{-1}) was determined using the equation,

$$O=(C_1-C_2)\,V\,T^{-1};$$

where C_1 and C_2 are oxygen concentrations (mg O_2 l^{-1}) in the chamber before and after each test, V is the volume (l) of the experimental chamber, and T is the duration (h) of the measurement period (Cech, 1990). To account for oxygen demand of the apparatus, 7–14 blanks were measured at each water temperature and season and subtracted from calculated metabolic rates (Cech, 1990).

Because metabolic rate of muskellunge varies with body size (Bevelhimer *et al.*, 1985) and mean size of age-0 muskellunge varied across seasons (Table I), weight-adjusted metabolic rate was used to account for allometric differences. Using a weight-dependent coefficient reported in Bevelhimer *et al.* (1985), absolute metabolic rate was divided by fish mass (W) to the power 0·82. Weight-adjusted, routine metabolic rates (mg O_2 h^{-1} $W^{-0{\cdot}82}$) were compared using a two-way analysis of variance with season and water temperature as grouping factors. For the two-way analysis of variance, multiple comparisons were made using least square means and significance level probabilities were adjusted using the Bonferroni procedure (SAS Institute, 1988).

RESULTS

Weight-adjusted metabolic rate varied significantly with water temperature and season (Fig. 1, Table II). Routine metabolic rate increased with increasing water temperature and ranged from 0·15 (winter at 5° C) to 0·39 mg O_2 h^{-1} $W^{-0{\cdot}82}$ (spring at 25° C). Similarly, metabolic rate varied significantly with season and was higher for juvenile muskellunge measured in spring and autumn than for fish tested in winter months (multiple comparison test, $P<0{\cdot}016$; Fig. 1).

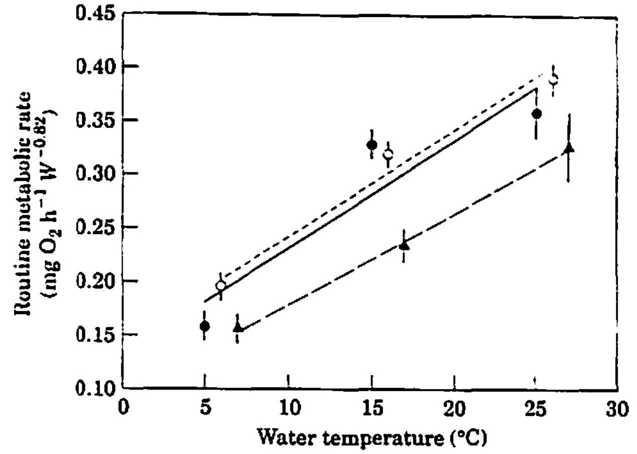

FIG. 1. Weight-adjusted, routine metabolic rate of age-0 muskellunge measured in the spring (○), autumn (●) and winter (▲) at 5, 15 and 25° C. Vertical bars represent 95% CL.

TABLE II. Summary statistics for analysis of variance tests of effects of temperature and season on routine metabolism of age 0 muskellunge

Source of variation	d.f.	Sum of squares	*F*	*P*
Temperature	2	0·53	97·06	0·0001
Season	2	0·06	10·32	0·0001
Interaction	4	0·02	2·10	0·09
Error	83	0·23		

Lack of a strong interaction between season and water temperature (P=0·09) implied that routine metabolic rate increased similarly with water temperature across seasons (Table II). For the range of water temperatures examined (5–25° C), Q_{10} values were calculated as:

$$Q_{10}=(K_2\,K_1^{-1})^{10(T_2-T_1)^{-1}}$$

where K_2 is metabolic rate at temperature T_2 and K_1 is metabolic rate at temperature T_1. Q_{10} values were similar across seasons at 1·43, 1·50, and 1·46 for spring, autumn and winter. Moreover, activity level, as measured by the coefficient of variation, was not correlated to routine oxygen consumption at 5° C (correlation analysis, r=0·25, P=0·14), 15° C (r= −0·08, P=0·62) or 25° C (r=0·17, P=0·41), implying that activity of fish was not a significant source of variation in seasonal measures of oxygen consumption.

DISCUSSION

Seasonal changes in fish metabolism have been identified for a variety of taxa (Winberg, 1956; Evans *et al.*, 1962; Burns, 1975; Evans, 1984) and are often attributed to gonadogenesis associated with the reproductive period (Beamish, 1964; Adams & Parsons, 1998). The observation that seasonal changes in metabolic rate occurred among immature fish suggests factors other than gonad development may also affect seasonal metabolism in muskellunge. This suggestion is supported further by the observation that metabolic rates in autumn were significantly higher than metabolic rates in winter. Higher oxygen consumption in autumn is out of phase with the reproductive cycle of muskellunge (e.g. spring spawning season), supporting the metabolic compensation hypothesis (Fry, 1964). Secondly, metabolic measurements made in autumn were generally intermediate to spring and winter observations which would be expected if metabolic compensation is an adaptation to the annual temperature cycle (Evans, 1984).

Photoperiod is believed to be a major exogenous cue regulating reproductive cycles in fishes (Kaya & Hasler, 1972; Kaya, 1973; Burns, 1976) and may be the primary cue initiating seasonal changes in metabolic rate. For example, juvenile Atlantic salmon reared at 10° C exhibited reduced oxygen consumption when exposed to decreased photoperiod (Withey & Saunders, 1973). Similarly, in a detailed study of adult pumpkinseed sunfish *Lepomis gibbosus* L., seasonal changes in metabolic rate were attributed to an anticipatory response to environmental conditions that was presumably initiated by photoperiod (Evans, 1984). In winter months, reduced metabolic rate in adult pumpkinseeds coincided with low water temperatures and low prey availability, a response analogous to hibernation in endotherms (Rea & Costa, 1992). The idea that some fishes undergo metabolic compensation as an anticipatory response to seasonally variable environmental conditions is supported further by the findings with immature muskellunge.

Evidence for seasonal metabolic compensation, while apparent in some fishes, remains variable across taxa. Metabolic rate of juvenile lake charr *Salvelinus namaycush* (Walbaum) and walleye *Stizostedion vitreum* (Mitchill) was not significantly correlated with season for fish examined at 8 and 12° C (Beamish, 1990). In contrast, metabolic rate of juvenile bluegill *Lepomis macrochirus* Rafinesque changed seasonally, but was higher in winter than in spring or summer periods (Wohlschlag & Juliano, 1959). In a subsequent review of Wohlschlag & Juliano (1959), Evans (1984) believed that elevated metabolic rates in winter months were an artifact of the experimental protocol since oxygen consumption by bluegill was measured in the field within 1 h after capture. Large discrepancies are often reported among studies of fish metabolism and may be attributable to variable stress levels, differences among respirometers (Caulton, 1978; Cech, 1990) or variable analytical techniques (Ross & McKinney, 1988). Additional work with other species that avoids these methodological problems will be required to determine the generality of seasonal metabolic compensation in fishes.

Because of differences in seasonal timing of experiments, variation among weights of age 0 muskellunge was difficult to control without starving fish. However, specific metabolic rates were higher for fish measured in spring than for fish measured in winter months, despite larger size of fish used in the spring experiments. Because specific metabolic rate of fishes decreases with increasing weight, variation among seasonal metabolic rates appears to be conservative.

TABLE III. Variation in routine metabolic rates of age-0 muskellunge measured either across populations or across seasons at water temperatures ranging from 5 to 25° C

Temperature (° C)	Variation among populations (coefficient of variation)	Variation among seasons (coefficient of variation)
5	6·2	26·3
15	14·6	21·5
25	7·2	18·1

Data for six muskellunge populations were obtained from Clapp & Wahl (1996) whereas seasonal variation represents observations reported here for a single muskellunge population.

Hence, even larger differences would be expected, particularly between spring and winter periods, if fish were similar in size.

Seasonal variation in metabolic rate of fishes has important implications in energy budget studies. The use of single-season determinations of metabolic rate, typical in the development of most bioenergetic models (Kitchell *et al.*, 1977), can lead to erroneous estimates for periods other than when metabolism was actually measured (Feldmeth & Jenkins, 1973; Evans, 1984; Cunjak *et al.*, 1987; Wahl & Stein, 1991). Moreover, the influence of seasonal variation in metabolism would be expected to affect accuracy of bioenergetic estimates differentially, depending on when laboratory measurements were obtained. In the present example, measurements made in spring or autumn would overestimate metabolic demand of muskellunge in winter months. However, because metabolic rate is reduced at low temperatures, absolute errors in bioenergetic estimates would remain low relative to other times of the year. Conversely, measurements made in winter months, particularly at high water temperatures, would underestimate metabolic demand substantially and result in larger model error during summer months when water temperature and physiological rates are high.

In addition to seasonal variation in fish metabolism, diel variation in metabolic rate of fishes has been reported. Metabolic rate of Nile tilapia *Oreochromis niloticus* L. varied over 24-h periods with peaks occurring during daylight hours and lows occurring at night (Ross & McKinney, 1988). The magnitude of the daily respiratory cycle of Nile tilapia varied ± 20% around the mean value, implying appreciable diel variation in metabolic rate of this species. Hence, both seasonal and diel variation in metabolic rate of fishes could be important sources of error when not accounted for in energy budget determinations.

Physiological differences among geographically distinct muskellunge populations could also contribute to variation in estimates of routine metabolic rate (Koppelman & Philipp, 1986; Clapp & Wahl, 1996). At 10° C, routine metabolic rate of muskellunge from the Ohio River and Great Lakes drainages was lower than that of fish from the Mississippi River drainage (Clapp & Wahl, 1996). At other temperatures, however, few physiological differences were found among muskellunge populations (Clapp & Wahl, 1996). For age-0 muskellunge, interpopulation differences in routine metabolic rates were much less variable than seasonal differences at comparable water temperatures (Table III). Hence, seasonal variation in routine metabolic rate appears to be a more important consideration in developing energy budgets than physiological differences across muskellunge populations.

Seasonal variation in metabolic rate of age-0 muskellunge supports the metabolic compensation hypothesis (Fry, 1964; Evans, 1984). In the natural environment, water temperatures and prey availability can vary predictably on an annual cycle. Beyond a simple thermokinetic response, the ability to compensate for seasonally variable environmental conditions would be an adaptive physiological mechanism in fishes (Fry, 1964; Evans, 1984). In our study, two lines of evidence support the notion that muskellunge undergo seasonally mediated physiological changes as an anticipatory response to environmental conditions; first, use of immature fish suggests that factors other than gonadogenesis may affect seasonal metabolic rate and second, higher metabolic rates in autumn than in winter months could not be attributed to the annual reproductive cycle (e.g. spring) of muskellunge.

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References

Adams, S. R. & Parsons, G. R. (1998). Laboratory-based measurements of swimming performance and related metabolic rates of field-sampled smallmouth buffalo (*Ictiobus bubalus*): a study of seasonal changes. *Physiological Zoology* **71**, 350–358.

Beamish, F. W. H. (1964). Seasonal changes in the standard rate of oxygen consumption in fishes. *Canadian Journal of Zoology* **42**, 189–194.

Beamish, F. W. H. (1990). Metabolism and photoperiodicity in juvenile lake charr and walleye. *Environmental Biology of Fishes* **29**, 201–207.

Bevelhimer, M. S., Stein, R. A. & Carline, R. F. (1985). Assessing significance of physiological differences among three esocids with a bioenergetic model. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 57–69.

Burns, J. R. (1975). Seasonal changes in the respiration of pumpkinseed, *Lepomis gibbosus*, correlated with temperature, day length, and stage of reproductive development. *Physiological Zoology* **48**, 142–149.

Burns, J. R. (1976). The reproductive cycle and its environmental control in the pumpkinseed, *Lepomis gibbosus*. *Copeia* **1976**, 449–455.

Caulton, M. S. (1978). The effect of temperature and mass on routine metabolism in *Sarotherodon mossambicus*. *Journal of Fish Biology* **13**, 195–201.

Cech, J. J. Jr (1990). Respirometry. In *Methods for Fish Biology* (Schreck, C. B. & Moyle, P. B., eds), pp. 335–362. Bethesda, MD: American Fisheries Society.

Clapp, D. F. & Wahl, D. H. (1996). Comparison of food consumption, growth, and metabolism among muskellunge: an investigation of population differentiation. *Transactions of the American Fisheries Society* **125**, 402–410.

Cunjak, R. A., Curry, R. A. & Power, G. (1987). Seasonal energy budget of brook trout in streams: Implications of a possible deficit in early winter. *Transactions of the American Fisheries Society* **116**, 817–828.

Evans, D. O. (1984). Temperature independence of the annual cycle of standard metabolism in the pumpkinseed. *Transactions of the American Fisheries Society* **113**, 494–512.

Evans, R. M., Purdue, F. C. & Hickman, C. P. (1962). The effect of temperature and photoperiod on the respiratory metabolism of rainbow trout (*Salmo gairdneri*). *Canadian Journal of Zoology* **40**, 107–118.

Feldmeth, C. R. & Jenkins, R. M. (1973). An estimate of energy expenditure by rainbow trout *Salmo gairdneri* in a small mountain stream. *Journal of the Fisheries Research Board of Canada* **30**, 1755–1759.

Fry, F. E. J. (1964). Animals in aquatic environments: fishes. In *Handbook of Physiology: Section 4* (Dill, D. B., Adolph, E. F. & Wilber, C. G., eds), pp. 715–728. Washington, D.C.: American Physiological Society.

Kaya, C. M. (1973). Effects of temperature and photoperiod on seasonal regression of gonads of green sunfish, *Lepomis cyanellus*. *Copeia* **1973**, 369–373.

Kaya, C. M. & Hasler, D. A. (1972). Photoperiod and temperature effects on the gonads of green sunfish *Lepomis cyanellus*, during the quiescent, winter phase of its annual cycle. *Transactions of the American Fisheries Society* **101**, 270–275.

Kitchell, J. F., Stewart, D. J. & Weininger, D. (1977). Applications of a bioenergetics model to yellow perch *Perca flavescens* and walleye *Stizostedion vitreum*. *Journal of the Fisheries Research Board of Canada* **34**, 1922–1935.

Koppelman, J. B. & Philipp, D. P. (1986). Genetic applications in musklellunge management. In *Managing Muskies* (Hall, G. E., ed.). *American Fisheries Society Special Publication* **15**, 111–121.

Meakins, R. H. (1975). The effects of activity and season on the respiration of the three-spined stickleback, *Gasterosteus aculeatus*. *Comparative Biochemistry and Physiology* **51**, 155–157.

Rea, L. D. & Costa, D. P. (1992). Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiological Zoology* **65**, 97–111.

Ross, L. G. & McKinney, R. W. (1988). Respiratory cycles in *Oreochromis niloticus* L. measured using a six-channel microcomputer-operated respirometer. *Comparative Biochemistry and Physiology* **89**, 637–643.

SAS Institute (1988). *SAS/STAT User's Guide, Release 6.03*. Cary, North Carolina: SAS Institute.

Wahl, D. H. & Stein, R. A. (1991). Food consumption and growth of three esocids: field tests of a bioenergetics model. *Transactions of the American Fisheries Society* **120**, 230–246.

Winberg, G. G. (1956). Rate of metabolism and food requirements of fishes. *Fisheries Research Board of Canada, Translation Series* **194**, 1960.

Withey, K. G. & Saunders, R. L. (1973). Effect of a reciprocal photoperiod regime on standard rate of oxygen consumption of post-smolt Atlantic salmon *Salmo salar*. *Journal of the Fisheries Research Board of Canada* **30**, 1898–1900.

Wohlschlag, D. E. & Juliano, R. O. (1959). Seasonal changes in bluegill metabolism. *Limnology and Oceanography* **4**, 195–209.