

## NOTES

### Fish Energetics: Larger Individuals Emerge from Winter in Better Condition

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**Abstract.**—We tested the hypothesis that larger individuals in a temperate fish population emerge from winter in better energetic condition than do smaller individuals. We sampled adult male bluegills *Lepomis macrochirus* in Lake Opinicon, Ontario, after spring ice break and just before active feeding began. By extracting neutral and membrane-bound polar lipids, we estimated the energetic condition of each individual. We found that both the mass of lipids and the lipids per gram of body weight were significantly and positively correlated with body size. These results are attributed to the allometric relationships between body size and energy reserves and between body size and metabolic rate. Body size, therefore, profoundly affects energetic state, which may explain why individuals of different size vary in their reproductive behavior and survivorship.

In fishes there exist positive allometric relationships between body size and energy reserves and negative allometric relationships between body size and metabolic rate (Brett and Groves 1979; Shuter and Post 1990). Thus, in northern populations where individuals rely on stored energy reserves to survive the winter starvation period (Keast 1968), it is possible that larger fish emerge from winter in better energetic condition than smaller fish. We tested this hypothesis on a northern population of bluegill *Lepomis macrochirus*.

In our study population, bluegills do not feed appreciably from October through May (Keast 1977). We collected a sample of adult male bluegills in spring, after ice break but before active foraging began, and determined the energetic condition of each fish. The amount of stored lipids, thought to be the main source of energy for fish during the winter starvation period (Shul'man 1974; Black and Love 1986) and the major source of energy for reproduction in fish (Wootton et al. 1978; Reznick and Braun 1987), was used as a measure of male energetic condition. We predicted a positive relationship between individual body size and energetic condition.

This work is part of a larger study on the nesting behavior of male bluegills. Females were, therefore, not included in the study. However, we expect

the results to be the same for both sexes. Recent studies of several sunfish species have demonstrated a negative relationship between body size and nest date for both males (Ridgway et al. 1991; Wiegmann et al. 1992; Baylis et al. 1993) and females (Wiegmann et al. 1992; Danylchuck and Fox 1994). These patterns have been attributed to differences in energetic condition among individuals, but no test of a correlation between energy level and body size after emergence from winter has been made.

#### Methods

A sample of 21 free-swimming adult male bluegills of parental size (Gross 1982) was collected by seine from the littoral zone at Lake Opinicon, Ontario, on 21 and 22 May 1994. Ice break on the lake occurred on about 21 April, and because of a cold spring, the bluegills had just begun to enter the shallows to feed at the time of sampling. This we verified upon finding their stomachs empty. We recorded the total length (tip of jaw to extended caudal fin) and wet weight of each individual and five scales were removed for aging. The fish were then wrapped in aluminum foil to prevent desiccation and frozen for transport to our laboratory in Toronto.

Each fish was partially thawed, and the complete body was ground into a homogenous mixture with a mortar and pestle and sodium hydroxide. The fish were not dried because elevated temperatures can cause lipid decomposition (Randall et al. 1991). Instead, the homogenate was immediately soaked in 100–150 mL of solvent in a flat-bottom glass beaker and repeatedly stirred for 90 min. The solvent, a 1:1 (volume per volume) mixture of hexane and dichloromethane, extracts neutral and membrane-bound polar lipids from the homogenated tissue (Randall et al. 1991) and has been used in other studies of sunfish (Justus and Fox 1994). The solvent was separated from the remaining tissue by vacuum filtering in a Buchner funnel and collected in a preweighed 500-mL round-bottom

TABLE 1.—Multiple-regression statistics indicating the relative contributions and significance ( $P$ ) of body size (weight) and age (years) to the amount of lipids possessed by individual male bluegills ( $R^2 = 0.651$ ,  $F = 16.792$ ,  $P = 0.0001$ ).

Variable	Partial regression coefficient	$P$
Weight	1.369	0.0002
Age	-0.731	0.0217

flask. The solvent was evaporated with a rotovaporator, leaving only the lipids in the bottom of the flask, which was then weighed again. The mass of lipid extracted from each fish was calculated as the difference in flask weight.

To examine allometric relationships and to control for increasing variance, all variables were log transformed prior to analysis. To test the predicted relationship between energetic state and body size, we regressed extracted lipid mass against remaining tissue mass where the latter is the difference between total wet body weight and extracted lipid mass. Both variables are measures of mass or volume and should scale allometrically at a 1:1 ratio if there were no effect of body size on energetic condition (Schmidt-Nielsen 1984). A regression slope greater than one would indicate that larger males possess proportionally more lipids per gram of nonlipid body tissue than do smaller males.

### Results

The sample of adult male bluegills ranged from 149 to 206 mm in length, and from 58 to 175 g

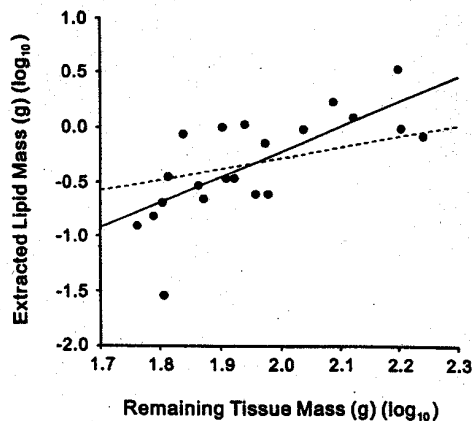


FIGURE 1.—Extracted lipid mass ( $y$ ) versus remaining tissue mass ( $x$ ) of individual male bluegills ( $N = 21$ ,  $r^2 = 0.517$ ,  $F = 20.34$ ,  $P = 0.0002$ ). Solid line is the regression line fitted to the data ( $y = -4.85 x^{2.32}$ ); the dashed line represents a slope of 1.

in wet weight. They were 7–10 years old. Length and weight were highly correlated ( $N = 21$ ,  $r^2 = 0.968$ ,  $P < 0.0001$ ), as were age and size (length:  $r^2 = 0.803$ ,  $P < 0.0001$ ; weight:  $r^2 = 0.811$ ,  $P < 0.0001$ ).

The mass of lipid extracted ranged greatly, from 0.029 to 3.261 g, among individuals. There was a highly significant and positive correlation between body size and lipid mass (length:  $N = 21$ ,  $r^2 = 0.471$ ,  $P = 0.0006$ ; weight:  $N = 21$ ,  $r^2 = 0.529$ ,  $P = 0.0002$ ). However, partial correlations revealed that total length was actually only spuriously correlated with lipid mass through its relationship with weight (lipid mass versus weight, length controlled:  $pr = +0.399$ ; lipid mass versus length, weight controlled:  $pr = -0.238$ ). Multiple-regression analysis revealed that body weight explained most of the variance in lipid mass found among individuals whereas age accounted for a smaller although significant proportion of the variance (Table 1).

As predicted, larger individuals were in better energetic condition than smaller individuals; larger individuals possessed proportionally more lipids (Figure 1;  $N = 21$ ,  $r^2 = 0.517$ ,  $P = 0.0002$ ). Lipid and remaining tissue mass did not scale 1:1; rather, the relationship had a slope greater than one ( $b = 2.32$ , 95% confidence interval: 1.24–3.39). This finding indicates that larger individuals possessed significantly more lipids per gram of body tissue than did smaller individuals (the relationship remained significant with the outlier point omitted,  $b = 1.98$ , 95% confidence interval: 1.09–2.87).

### Discussion

Our results show that larger adult male bluegills emerge from the winter starvation period in better energetic condition than smaller adult male bluegills. The size-dependence of spring energetic condition is probably due to physiological allometry: positive allometric relationships between body size and energy reserves and negative allometric relationships between body size and metabolic rate (Brett and Groves 1979; Shuter and Post 1990). Larger male bluegills may store relatively more lipid energy before entering the winter or deplete relatively less of their store during the winter. Either or both would result in the relationship that we have found; our work cannot distinguish between these possibilities.

It is possible that the variation in energy with body size which we found may be due to factors other than physiological allometry. For example, larger individuals may feed during the winter.

However, studies of winter foraging by bluegills in Lake Opinicon and elsewhere show that only very limited feeding occurs, and usually by smaller, not larger, individuals (Keast 1968, 1977). It is interesting to note that physiological allometry might predict this feeding activity by smaller individuals. Another possibility is that larger individuals may begin feeding earlier after ice break than smaller individuals. However, we began sampling before any bluegills were feeding within the littoral zone and captured individuals as they arrived. There was no relationship in our sample between the date of capture and body size ( $t$ -tests; total length:  $t = -1.45$ ,  $P = 0.164$ ; weight:  $t = -1.30$ ,  $P = 0.211$ ) nor date of capture and energetic or body condition ( $t$ -tests; extracted lipids:  $t = -0.76$ ,  $P = 0.258$ ; % lipids:  $t = 0.15$ ,  $P = 0.885$ ; body condition:  $t = -1.23$ ,  $P = 0.235$ ).

A third possibility is that the greater energy reserves of larger individuals may be due to behavioral differences associated with body size that are independent of allometric physiology. For example, if larger individuals face less predation risk, they may consume more prey items than do smaller individuals, and thus build up a greater energy reserve prior to the winter irrespective of allometric physiology. However, the bluegills in our sample are larger than those consumed by the Lake Opinicon predators, which include largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, and northern pike *Esox lucius* (Gross and MacMillan 1981; M. R. Gross, unpublished data). Finally, our technique of lipid extraction does not extract covalently bound lipids; perhaps smaller individuals store a greater proportion of their lipids as covalently bound lipids. However, covalently bound lipids are a relatively unimportant energy source. In freshwater fish, lipid energy is stored primarily as fats known as triacylglycerols (Davenport and Johnson 1971; Hadley 1985), the neutral lipids which are extracted by our technique. Thus, our measurement of energy should not be affected by covalently bound lipids. In conclusion, we consider the physiological allometric relationships between metabolic rate and energetics (Brett and Groves 1979; Shuter and Post 1990) to be the most likely explanations for the data.

Our results may have general applicability for understanding the reproductive behavior and survivorship of fishes. For example, they confirm the energy linkage with body size that has been postulated to explain why larger individuals of both sexes breed earlier than smaller individuals (e.g.,

Ridgway et al. 1991; Danylchuck and Fox 1994) and they support the idea that energetic variance may be important in overwinter survival, such as in the relationship between body size and survival in young-of-the-year fish (e.g., Oliver et al. 1979; Toney and Coble 1979; Post and Evans 1989; Cargnelli and Gross 1996).

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#### References

- Baylis, J. R., D. D. Wiegmann, and M. H. Hoff. 1993. Alternating life histories of smallmouth bass. *Transactions of the American Fisheries Society* 122:500-510.
- Black, D., and R. M. Love. 1986. The sequential mobilisation and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. *Journal of Comparative Physiology B* 156:469-479.
- Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pages 279-352 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*, volume 8. Academic Press, New York.
- Cargnelli, L. M., and M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:360-367.
- Danylchuck, A. J., and M. G. Fox. 1994. Age and size-dependent variation in the seasonal timing and probability of reproduction among mature female pumpkinseed, *Lepomis gibbosus*. *Environmental Biology of Fishes* 39:119-127.
- Davenport, J. B., and A. R. Johnson. 1971. The nomenclature and classification of lipids. Pages 1-28 in A. R. Johnson and J. B. Davenport, editors. *Biochemistry and methodology of lipids*. Wiley, New York.
- Gross, M. R. 1982. Sneakers, satellites and parents: polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie* 60:1-26.
- Gross, M. R., and A. M. MacMillan. 1981. Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology and Sociobiology* 8:163-174.
- Hadley, N. F. 1985. *The adaptive role of lipids in biological systems*. Wiley, New York.
- Justus, J. A., and M. G. Fox. 1994. The costs of early maturation on growth, body condition and somatic

- lipid content in a lake pumpkinseed (*Lepomis gibbosus*) population. *Ecology of Freshwater Fish* 3: 9-17.
- Keast, A. 1968. Feeding of some Great Lakes fishes at low temperatures. *Journal of the Fisheries Research Board of Canada* 25:1199-1218.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition between two Centrarchid fishes. *Evolutionary Biology* 10: 333-395.
- Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108:130-136.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1958-1968.
- Randall, R. C., H. Lee II, R. J. Ozretich, J. L. Lake, and R. J. Pruell. 1991. Evaluation of selected lipid methods for normalizing pollutant bioaccumulations. *Environmental Toxicology and Chemistry* 10: 1431-1436.
- Reznick, D. N., and B. Braun. 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as reproductive adaptation. *Oecologia* 73:401-413.
- Ridgway, M. S., B. J. Shuter, and E. E. Post. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Journal of Animal Ecology* 60:665-681.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge University Press, New York.
- Shulman, G. E. 1974. *Life cycles of fish*. Wiley, New York.
- Shuter, B. J., and J. R. Post. 1990. Climate, population variability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314-336.
- Toneys, M. L., and D. W. Coble. 1979. Size-related first winter mortality of freshwater fishes. *Transactions of the American Fisheries Society* 108:415-419.
- Wiegmann, D. D., J. R. Baylis, and M. H. Hoff. 1992. Sexual selection and fitness variation in a population of smallmouth bass *Micropterus dolomieu* (Pisces: Centrarchidae). *Evolution* 46:1740-1753.
- Wootton, R. J., G. W. Evans, and L. Mills. 1978. Annual cycle in female three-spined sticklebacks (*Gasterosteus aculeatus*) from an upland and lowland population. *Journal of Fish Biology* 12:331-343.

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