

Scale strength as a cost of rapid growth in sunfish

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Comparisons among populations have revealed adaptive variation in growth rate within several species. However, theoretical models suggest that a cost to rapid growth must exist in order to explain why some populations grow slowly. Based on previous work with development of the cranial skeleton in pumpkinseed sunfish, we proposed that rapid growth may compromise the strength of all skeletal elements in vertebrates. Using pumpkinseed from six populations known to differ in their intrinsic growth rates, we correlated strength of scales, in terms of resistance to penetration, with individual growth rate. We found a negative correlation that was consistent both within and among populations. This trade-off between growth rate and scale strength may have fitness consequences in terms of likelihood of surviving predation attempts or swimming efficiency.

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Species vary widely in growth rates and this variation is often thought to be adaptive (Grime and Hunt 1975, Case 1978, Arendt 1997). Recently, several examples of adaptive variation in growth rate have also been demonstrated within species (e.g., Conover and Present 1990, Gotthard et al. 1994, Arendt and Wilson 1999). Rapid growth may be favored for several reasons including attaining a size refuge from predation or competition, or reaching a minimum size for overwinter survival (reviewed in Arendt 1997). However, these factors cannot explain why other species or populations maintain slow growth rates (Starck 1994, Arendt and Wilson 1997). Theoretical work suggests that growth rates will always be at their physiological maximum unless there exists some intrinsic cost of rapid growth (Case 1978, Sibly et al. 1985, Abrams et al. 1996, Arendt and Wilson 1997). There is evidence that few organisms normally grow at their physiological maximum (Callow 1982), so a primary task of studying growth rate evolution is to identify costs of rapid growth.

Potential costs of rapid growth can be roughly grouped as 1) behavioral, 2) physiological, or 3) developmental. Behavioral costs include increased risk tak-

ing in order to obtain enough food to sustain rapid growth (e.g., Werner 1994, Abrahams and Sutterlin 1999). Physiological costs arise from allocation of resources to growth that would normally be used for other functions. Such functions may include starvation resistance (Gotthard et al. 1994), protein turnover (e.g., Morgan et al. 2000), or metabolic efficiency (Stevens et al. 1998, McCarthy 2000). Development may compromise rapid growth because most cells lose the ability to divide and contribute further towards growth once they differentiate and take up their mature function (Starck and Ricklefs 1998). Development of thermoregulatory ability is inversely correlated with growth rate among species of birds (Visser and Ricklefs 1993, Ricklefs et al. 1994). Skeletal development also appears to be inversely related to growth rate among species of birds (Carrier and Leon 1990, Starck 1994, 1998).

Recently, we showed that a fast growing strain of pumpkinseed sunfish (*Lepomis gibbosus*) had a delayed onset of mineralization in their cranial bones relative to a slow growing strain (Arendt and Wilson 2000). The sequence in which bones ossify was consistent between strains, but each bone first showed signs of calcium deposition approximately two days later in the fast

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strain than in the slow strain. This means that the fast growing fish were both older and larger when they had the same degree of ossification. Although this suggests a trade-off between growth rate and skeletal development, we do not know if this difference persists throughout life or if this trade-off actually translates into a fitness cost of rapid growth. Arendt and Wilson (2000) suggested that delayed mineralization may result in weaker scales and fin spines. This, in turn, should result in decreased protection against predation. In addition, scales contribute to the stiffness of skin which is important in swimming efficiency (Wainwright 1983, McHenry et al. 1995, Long et al. 1996).

The goal of this study is to correlate scale strength with differences in intrinsic growth rate of pumpkinseed sunfish. This extends the findings of Arendt and Wilson (2000) by examining a post-cranial skeletal structure at an older age. In addition, Arendt and Wilson (2000) compared just two strains. This study examines a total of six populations, three fast-growing and three slow-growing, in order to show that the trade-off between rapid growth and skeletal development is general in pumpkinseed sunfish (see Arendt and Wilson 1997 for information on why pumpkinseed populations differ in intrinsic growth rate).

Materials and methods

Brood stock

In the spring of 1995, adults (10 male and 10 female per lake) were collected from five lakes in southern Ontario, Canada and one lake in northeastern Pennsylvania and stocked into separate ponds at the experimental pond facility at Cornell University. The Pennsylvania population replaced a sixth Ontario population which did not survive stocking (see Arendt and Wilson 1997 for details). Bluegill sunfish are present in three of these populations but absent from the other three. Pumpkinseed derived from populations sympatric with bluegill have evolved a faster growth rate than pumpkinseed from populations lacking bluegill (Arendt and Wilson 1997, 1999) allowing them to reach a size-refuge from competition (Mittelbach 1984). Throughout this paper, the term "sympatric pumpkinseed" refers to those that have had an evolutionary history of competition with bluegill, and "allopatric pumpkinseed" refers to those that have no evolutionary history of competition. However, all fish were raised under common monospecific conditions so differences reflect genetic differentiation.

Measurement of growth rate and scale strength

Young-of-year were collected from breeding ponds in the fall of 1996 using a seine net, transferred to 76-L

aquaria and maintained at 18°C with a 14L:10D photoperiod. Fish were allowed to acclimate to laboratory conditions for two months. To measure growth rates, individual fish were isolated in 38-L aquaria divided into quarters with clear Plexiglas. Each aquarium held four fish from the same population, four aquaria for each of the six populations. The sides of the aquaria were covered so that other aquaria were not visible. This design reflects a number of considerations. Fish growth is often influenced by social factors so intrinsic growth rate is best measured in isolated fish. However, pumpkinseeds are a gregarious species that do not behave normally in isolation. We did not mix populations within an aquarium because sympatric and allopatric pumpkinseed react differently to dominance interactions (unpubl. data). The Plexiglas dividers were not sealed and allowed visual and olfactory contact among fish from the same population without allowing physical contact. This seemed the best compromise between complete isolation and complete contact. Fish were fed approximately 1% wet weight of a commercial diet (Hikari Cichlid Gold pellets). Standard lengths (from nose to posterior end of caudal peduncle) were measured five times throughout the winter and instantaneous growth rates calculated for each interval as $IGR = [\log(\text{length}_2) - \log(\text{length}_1)] / (\text{time}_2 - \text{time}_1)$. The average of these intervals was used as each individual's growth rate.

Fish ranged in size from 32.0 to 40.0 mm standard length when scales were taken. Scales were taken from a standard location on the left side of each fish determined by laying the pectoral fin flat against the body. A cluster of four to eight scales was removed from just behind the tip of the pectoral fin and ventral to the lateral line using sterile tweezers. Scales were stored in 1-mm microcentrifuge tubes filled with de-ionized water. Algal growth occurred in some tubes before scales could be analyzed and these samples were discarded.

We measured scale strength as resistance to being pierced with a needle. Scales were placed on a stainless steel plate and dried under a 100-W bulb for five min. After drying, each scale was checked under a dissecting scope to determine that only one scale was present, that the scale had dried flat, and to check for signs of regeneration. When a scale is lost by a fish, a new scale grows to replace it within a few days (Mugiya 1980). Normally, scales of temperate fish contain a series of rings corresponding to annual growth periods. Regenerated scales are typically the same size as non-regenerated scales, but contain an amorphous center region corresponding to the period of rapid scale growth. We expected that this difference in structure would cause regenerated scales to be less resistant to piercing than non-regenerated scales. We tested this possibility by comparing regenerated scales to non-regenerated scales from a given fish. Resistance to piercing was measured using a steel sewing needle fixed to the bottom of a

glass tube capped with a funnel (Fig. 1). The tube rested within a sleeve of PVC piping that clamped to a ring stand, allowing vertical movement but no lateral movements. The needle was placed on the center of the scale and ball bearings added to the funnel until the needle just pierced the scale. The apparatus was wired so that a buzzer sounded as soon as the needle pierced the scale and contacted the steel plate completing the circuit. The weight of the ball bearings was used as the mass needed to pierce a given scale. Throughout sampling, we periodically checked scales after measurement to confirm that the needle had been placed in the center of the scale. Any scales with poor placement were redone. Reliability of the apparatus was measured by repeatedly piercing several scales. The differences between measures for a given scale were compared to the total variation among scales from the same fish. We estimate that variation in measurements add less than 4% to the total variation estimated for a single fish. To control for the possibility that the needle used to pierce scales might become blunt over time, we randomized the order in which fish were analyzed. The use of order as a covariate did not significantly improve our ability to detect scale strength, so this factor was dropped.

Statistical analysis

Growth rates were compared using a nested analysis of variance with population nested within competitive history (sympatric vs. allopatric populations). A similar analysis was conducted on scale strength, coupled with

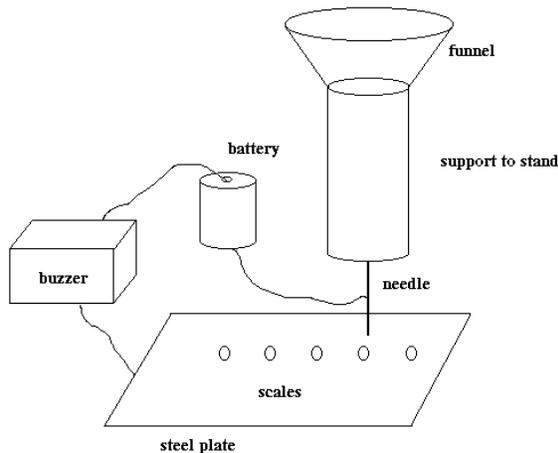


Fig. 1. Apparatus used to measure scale resistance to penetration. Scales were placed on the steel plate and allowed to adhere by drying for 5 min. The needle was placed on the center of a given scale and ball bearings added to the sealed funnel at the top. The plate was wired to one end of a buzzer, and the needle to the other end so that the buzzer would sound when the needle pierced the scale and made contact with the plate.

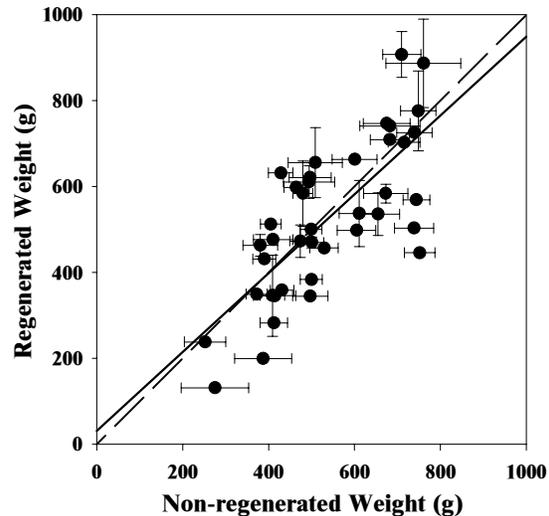


Fig. 2. Mean weight that regenerated scales could hold in comparison to the mean weight that normal scales from the same fish could hold. Solid line is the regression through these values, dashed line represents equivalent weight for regenerated and non-regenerated scales. Error bars = SEM.

analysis of covariance to determine the effect of competitive history independent of growth rate. Because fish within a given aquarium were from the same population, results based on individual values may be confounded with aquarium effects. We controlled for this by averaging growth rates and scale strengths for all fish within an aquarium. We report on these mean values, although patterns based on individual scores gave similar results.

Results

Forty of the 90 fish analyzed for scale strength had one or more regenerated scales. Regenerated scales were not significantly different from non-regenerated scales in resistance to piercing (Wilcoxon paired sign ranks $T = 365$, $N = 40$, $p > 0.05$) (Fig. 2). We therefore pooled all scales for further analysis.

The weight scales could withstand before being pierced ranged from 397 to 1112 g with an average of 772 g. Overall, sympatric pumpkinseed grew significantly faster (mean \pm SE were 8.54 ± 0.24 %/d) than allopatric pumpkinseed (6.86 ± 0.20 %/d) as expected from our previous research ($F_{1,4} = 11.0$, $p = 0.03$). There was no difference among the three sympatric populations or the three allopatric populations ($F_{4,18} = 0.9$, $p = 0.5$). As predicted, sympatric pumpkinseed also had significantly weaker scales (mean \pm SE; 498.3 ± 27.0 g) than allopatric fish (559.7 ± 27.9 g) ($F_{1,4} = 18.1$, $p = 0.01$), again with no difference among populations within competitive history ($F_{4,17} = 0.3$, $p = 0.86$). The

results of the ANCOVA, using growth rate as the covariate, indicate that this effect was due entirely to the difference in growth rate (main effect of competitive history $F_{1,4} = 0.8, p = 0.4$; effect of growth rate as covariate $F_{1,4} = 15.4, p = 0.02$), and does not reflect fundamental differences between sympatric and allopatric pumpkinseed. Regressions of scale strength on growth rate had similar slopes for both competition types ($p > 0.1$). With all fish combined, growth rate showed a highly significant negative correlation with scale strength ($p < 0.01$), explaining 45.7% of the variation in scale strength (Fig. 3). Scale strength depended only on growth rate, not the size of fish at the time scales were removed, as fish length did not significantly improve the regression model.

Discussion

Our data show that scale strength, in terms of ability to resist being pierced, is compromised by rapid growth. These results match what we had predicted based on patterns of skeletal ossification (Arendt and Wilson 2000). The ANCOVA results suggest that differences among populations are due entirely to differences in growth rate. That is, selection for rapid growth in response to competition with bluegill has not imposed an additional cost on scale strength beyond that normally found within a population. These results suggest that rapid growth compromises development of post-cranial skeletal elements as well as cranial bones. In addition, this effect is important at least through most

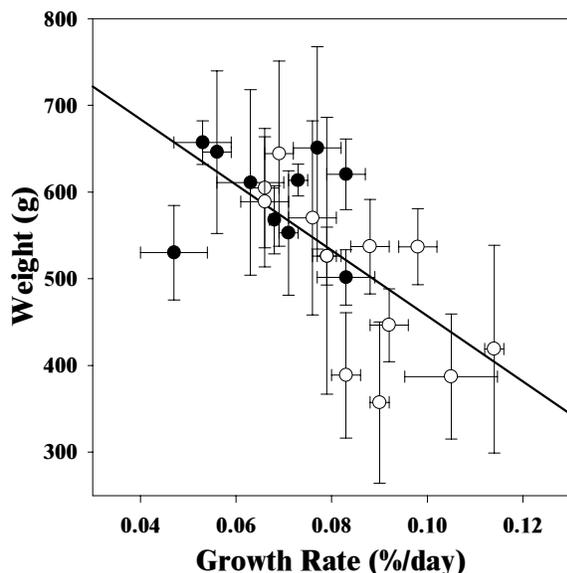


Fig. 3. Average strength of scales by average growth rate of the four fish within each aquarium for sympatric (open circles) and allopatric (closed circles) pumpkinseed. Regression for all fish combined (weight = $835.88 - 3788 \times \text{IGR}$; $p < 0.001$; $r^2 = 0.46$)

of the first year of life as fish used in this study were 8-10 months old, as opposed to Arendt and Wilson (2000) which only followed fish through the first 8 weeks after hatching.

Several mechanisms may explain the trade-off between growth rate and scale strength. Starck (1994, 1998) has argued that skeletal development is delayed in fast growing species of bird relative to slower growing species because of a general trade-off between cellular proliferation and differentiation (see Arendt 2000). As a result, bones (and scales) will be weaker in fast growing individuals throughout ontogeny, but should equalize late in ontogeny when growth begins to slow. Alternatively, the strength of skeletal elements may be limited by the rate at which inorganic minerals can accumulate. Palmer (1981) argued that growth rates in gastropods are limited by the rate at which calcium carbonate can be deposited in the shell. A rate limit on mineralization of shell material means that fast growing snails must have either thinner or more porous shells than slow growers (Palmer 1981, Boulding and Hay 1993). Deposition of calcium phosphate in vertebrate skeletons is similar to that of calcium carbonate in mollusk shells (Dacke 1979, Anderson 1985). This is an inorganic process, the rate depending upon temperature and ion concentration and little influenced by the organism. If the rate of mineralization is similar for fast and slow growing individuals, then rapid growth will result in a greater proportion of collagen resulting in weaker skeletal elements. Finally, weaker scales may simply be the result of differential allocation of calcium to metabolic demands and away from skeletal elements in fast growing individuals. Metabolic requirements for calcium may increase in fast growing individuals in order to compensate for the reduced efficiency of enzymes as protein turnover decreases (Hawkins 1991, Morgan et al. 2000) or to meet increased metabolic rates (McCarthy 2000). Flik et al. (1993) argued that treatment of tilapia (*Oreochromis mossambicus*) with growth hormone had little effect on calcium metabolism. However, fish treated with growth hormone did have lower calcium concentrations in both scales and bones than three groups of control fish (scales: 4.80 ± 0.62 vs. 5.15 ± 0.52 mmol/g, bones: 5.04 ± 0.36 vs. 5.20 ± 0.45 mmol/g). These differences were not significant, but with only nine fish per group it would be very difficult to statistically pick up differences of this level. These mechanisms for weaker bones/scales in fast growing individuals are not mutually exclusive and future work will be needed to determine which contribute to the trade-off we report here.

We were surprised to find that regenerated scales were similar in strength to non-regenerated scales. Normal scale growth is strongly correlated with whole body growth in sunfish so that annual deposition of material around the margin of a scale can be used to estimate annual growth increments (e.g., Osenberg et al. 1988,

Fox 1994). This means that faster somatic growth translates directly into faster scale growth. Because lost scales are replaced over a period of days to weeks (Mugiya 1980) rather than months to years, we expected the much faster growth of regenerated scales to translate into especially weak scales. The fact that regenerated scales appear to match the strength of normal scales suggests that regeneration depends upon mechanisms that do not incur the same cost to strength seen when comparing across individuals. This cost may be alleviated if regenerated scales are thicker than non-regenerated scales, or if the actual growth process differs. When scales are lost, regeneration appears to get priority in calcium allocation over other processes (Weiss and Watabe 1978, Mugiya 1980, Takagi et al. 1989), suggesting that maintaining scale strength has an important fitness function.

The functional role of scales is, unfortunately, not well understood. We have assumed that scales play an important role in protecting fish from predators. Scarring indicative of failed predation attempts are fairly common in small fish (Smith and Lemly 1986, Reist et al. 1987, Reimchen 1988). Scale strength undoubtedly plays an important role in determining the amount of damage sustained by survivors of predation events. We measured resistance to piercing because this type of injury is typical of predatory fish (Reimchen 1988), although other factors are likely to be important (e.g., some fish "shed" scales during predation attempts). Others have argued that the role of scales as armor is relatively unimportant (e.g., Aleyev 1977) and that they play a greater role in swimming efficiency. Aleyev (1977) emphasized the importance of scale microstructure in breaking up the boundary layer and reducing drag, a function that is probably not affected by scale strength. In addition, scales likely contribute to skin stiffness, which is important in determining the efficiency with which muscle contraction translates into forward motion (McHenry et al. 1995, Long et al. 1996). The same would be true if strength of the internal skeleton is also compromised by rapid growth (see Arendt and Wilson 2000). This may in part explain the trade-off between growth rate and critical swimming speed recently found in several species of fish (Kolok and Oris 1995, Farrell et al. 1997, Gregory and Wood 1998). If the trade-off between growth rate and scale strength holds for all skeletal elements in fish, feeding efficiency may be severely compromised in molluscivores such as pumpkinseed sunfish and some cichlids. These species crush their prey between two bones in the back of their throats (Lauder 1983, Liem and Kaufmann 1984). If these bones have a low density due to rapid growth, then fast growing fish will be confined to smaller snails or those species with relatively weak shells (Wainwright et al. 1991).

Our results demonstrate a clear trade-off between growth rate and scale strength. However, given our

ignorance about the functional significance of scale strength in fish, we cannot be certain this translates directly into a fitness cost for fast growing fish. Coupled with previous work on early development of the cranial skeleton (Arendt and Wilson 2000), we suggest it is likely rapid growth compromises skeletal strength in general. Moreover, we now know that variation in scale strength exists among individuals within a population, giving us the variation necessary to test hypotheses for the role of scales in fish.

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References

- Abrahams, M. V. and Sutterlin, A. 1999. The foraging and antipredator behaviour of growth-enhanced transgenic Atlantic salmon. - *An. Behav.* 58: 933-942.
- Abrams, P. A., Leimar, O., Nylin, S. and Wiklund, C. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. - *Am. Nat.* 147: 381-395.
- Aleyev, Y. G. 1977. Nekton. - Junk.
- Anderson, H. C. 1985. Normal biological mineralization. - In: Rubin, R. P., Weiss, G. B. and Putney, J. J. W. (eds), *Calcium in biological systems*. Plenum Press, pp. 599-606.
- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. - *Q. Rev. Biol.* 72: 1-29.
- Arendt, J. D. 2000. Allocation of cells to proliferation vs. differentiation and its consequences for growth and development. - *J. Exp. Zool. (Mol. Develop. Evol.)* 288: 219-234.
- Arendt, J. D. and Wilson, D. S. 1997. Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). - *Evolution* 51: 1946-1954.
- Arendt, J. D. and Wilson, D. S. 1999. Countergradient selection for rapid growth in pumpkinseed sunfish: disentangling ecological and evolutionary effects. - *Ecology* 80: 2793-2798.
- Arendt, J. D. and Wilson, D. S. 2000. Population differences in the onset of cranial ossification in pumpkinseed (*Lepomis gibbosus*), a potential cost of rapid growth. - *Can. J. Fish. Aquat. Sci.* 57: 351-356.
- Boulding, E. G. and Hay, T. K. 1993. Quantitative genetics of shell form of an intertidal snail: constraints on short-term response to selection. - *Evolution* 47: 576-592.
- Calow, P. 1982. Homeostasis and fitness. - *Am. Nat.* 120: 416-419.
- Carrier, D. and Leon, L. R. 1990. Skeletal growth and function in the California gull (*Larus californicus*). - *J. Zool.* 222: 375-389.
- Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. - *Q. Rev. Biol.* 53: 243-282.
- Conover, D. A. and Present, T. M. C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. - *Oecologia* 83: 316-324.
- Dacke, C. G. 1979. Calcium regulation in sub-mammalian vertebrates. - Academic Press.
- Farrell, A. P., Bennett, W. and Devlin, R. H. 1997. Growth-enhanced transgenic salmon can be inferior swimmers. - *Can. J. Zool.* 75: 335-337.

- Flik, G., Atsma, W., Fenwick, J. C. et al. 1993. Homologous recombinant growth hormone and calcium metabolism in the tilapia, *Oreochromis mossambicus*, adapted to fresh water. - J. Exp. Biol. 185: 107-119.
- Fox, M. G. 1994. Growth, density, and interspecific influences on pumpkinseed sunfish life-histories. - Ecology 75: 1157-1171.
- Gotthard, K., Nylin, S. and Wiklund, C. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. - Oecologia 99: 281-289.
- Gregory, T. R. and Wood, C. M. 1998. Individual variation and the interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). - Can. J. Fish. Aquat. Sci. 55: 1583-1590.
- Grime, J. P. and Hunt, R. 1975. Relative growth rate: its range and adaptive significance in a local flora. - J. Ecol. 63: 393-422.
- Hawkins, A. J. S. 1991. Protein turnover: a functional appraisal. - Funct. Ecol. 5: 222-233.
- Kolok, A. S. and Oris, J. T. 1995. The relationship between specific growth rate and swimming performance in male fathead minnows (*Pimephales promelas*). - Can. J. Zool. 73: 2165-2167.
- Lauder, G. V. 1983. Functional and morphological bases of trophic specialization in sunfishes (Teleostei, Centrarchidae). - J. Morphol. 178: 1-21.
- Liem, K. F. and Kaufman, L. S. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. - In: Echelle, A. B. and Kornfield, I. (eds), Evolution of Fish Species Flocks. Univ. of Maine at Orono Press, pp. 203-215.
- Long, J., John H., Hale, M. E. et al. 1996. Functions of fish skin: flexural stiffness and steady swimming of longnose gar *Lepisosteus osseus*. - J. Exp. Biol. 199: 2139-2151.
- McCarthy, I. D. 2000. Temporal repeatability of relative standard metabolic rate in juvenile Atlantic salmon and its relation to life history variation. - J. Fish Biol 57: 224-238.
- McHenry, M. J., Pell, C. A. and Long, J. H. 1995. Mechanical control of swimming speed: stiffness and axial wave form in undulating fish models. - J. Exp. Biol. 198: 2293-2305.
- Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). - Ecology 65: 499-513.
- Morgan, I. J., McCarthy, I. D. and Metcalfe, N. B. 2000. Life-history strategies and protein metabolism in overwintering juvenile Atlantic salmon: growth is enhanced in early migrants through lower protein turnover. - J. Fish Biol 56: 637-647.
- Mugiya, Y. 1980. The source of calcium in regenerating scales of the goldfish, *Carassius auratus*. - Comp. Biochem. Physiol. 66A: 521-524.
- Osenberg, C. W., Werner, E. E., Mittelbach, G. G. and Hall, D. J. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. - Can. J. Fish. Aquat. Sci. 45: 17-26.
- Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? - Nature 292: 150-152.
- Reimchen, T. E. 1988. Inefficient predators and prey injuries in a population of giant stickleback. - Can. J. Zool. 66: 2036-2044.
- Reist, J. D., Bodaly, R. A., Fudge, R. J. P. et al. 1987. External scarring of whitefish, *Coregonus nasus* and *C. clupeaformis* complex, from western Northwest Territories, Canada. - Can. J. Zool. 65: 1230-1239.
- Ricklefs, R. E., Shea, R. E. and Choi, I.-H. 1994. Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: a constraint on evolutionary response. - Evolution 48: 1080-1088.
- Sibly, R., Calow, P. and Nichols, N. 1985. Are patterns of growth adaptive? - J. Theor. Biol. 112: 553-574.
- Smith, R. J. and Lemly, A. D. 1986. Survival of fathead minnows after injury by predators and its possible role in the evolution of alarm substance. - Environ. Biol. Fishes 15: 147-149.
- Starck, J. M. 1994. Quantitative design of the skeleton in bird hatchlings: does tissue compartmentalization limit posthatching growth rates? - J. Morphol. 222: 113-131.
- Starck, J. M. 1998. Structural variants and invariants in avian embryonic and postnatal development. - In: Starck, J. M. and Ricklefs, R. E. (eds), Avian growth and development. Oxford Univ. Press, pp. 59-88.
- Starck, J. M. and Ricklefs, R. E. (eds). 1998. Avian growth and Development. - Oxford Univ. Press.
- Stevens, E. D., Sutterlin, A. and Cook, T. 1998. Respiratory metabolism and swimming performance in growth hormone transgenic Atlantic salmon. - Can. J. Fish. Aquat. Sci. 55: 2028-2035.
- Takagi, Y., Hirano, T. and Yamada, J. 1989. Scale regeneration of Tilapia (*Oreochromis niloticus*) under various ambient and dietary calcium concentrations. - Comp. Biochem. Physiol. 92A: 605-608.
- Visser, G. H. and Ricklefs, R. E. 1993. Development of temperature regulation in shorebirds. - Physiol. Zool. 66: 771-792.
- Wainwright, S. A. 1983. To bend a fish. - In: Webb, P. W. and Weihs, D. (eds), Fish biomechanics. Praeger Scientific, pp. 68-91.
- Wainwright, P. C., Osenberg, C. W. and Mittelbach, G. G. 1991. Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. - Funct. Ecol. 5: 40-55.
- Weiss, R. E. and Watabe, N. 1978. Studies on the biology of fish bone I. Bone resorption after scale removal. - Comp. Biochem. Physiol. 60A: 207-211.
- Werner, E. E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. - Ecology 75: 197-213.