

Bioenergetics Modeling Approaches to Evaluation of Stress in Fishes

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Abstract.—Bioenergetics models that summarize the physiological energetics of growth are versatile and powerful tools for evaluating the effects of stress on fishes at the individual or population level. These models have usually been developed for "healthy" fish, but stressors may affect any component of the energy-budgeting process. Bioenergetics models can be used in two principal ways to detect or evaluate stress effects. One is to use a healthy-fish model as a null hypothesis to determine whether or not an observed growth pattern can be explained by natural causes without invocation of stress effects that alter the energy-budgeting process. Alternatively, known effects of stressors on feeding, metabolic rate, or other components of the energy budget can be incorporated directly into a model to simulate their indirect effects on growth. Bioenergetics modeling can serve as a short-term indicator of long-term stress. It can also be used to investigate chronic or transient stress and can reveal indirect or higher-order effects. Because mortality and reproduction are often size-dependent, bioenergetics models can reveal implications of stress for these processes. These models require substantial amounts of physiological data, but models already exist for many species. Comparisons between simulations of stressed and unstressed fish can provide valuable information even when our confidence in exact model predictions is low.

The effects of stress on fishes are manifested in three primary processes: mortality, growth, and reproduction. Bioenergetics modeling focuses on growth, which integrates all the biotic and abiotic factors influencing the fish. Changes in growth rate can be sensitive indicators of changes in a fish's food resource, habitat, or physiological condition. Bioenergetics models summarize the growth process, so they can be used to decompose an observed growth pattern and determine the separate effects of temperature, activity, feeding rate, and other variables on growth. Because mortality and reproduction are often strongly size-dependent, bioenergetics modeling can offer insights into the effects of stress on these processes as well.

Bioenergetics models summarize our knowledge of the growth process in a balanced energy budget, in which growth equals the energy consumed in food minus energy lost through respiration, specific dynamic action (SDA, the costs of processing food), egestion, and excretion. These components have been studied extensively for a wide array of fishes, and the general functional relationships are often very similar among species (Hewett and Johnson 1987). Specific respiration or metabolic rate ($\text{kJ} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) typically declines exponentially as fish size increases, and increases exponentially with increasing temperature and activity level. Maximum feeding rate also depends

on size and temperature, declining exponentially with increasing size and increasing with temperature up to an optimum temperature before declining. Actual food consumption depends on prey availability and maximum feeding rate. The remaining components of the energy budget depend largely on the amount and type of food eaten; they also may be influenced by temperature (Elliott 1976), but SDA, egestion, and excretion often are relatively constant proportions of the amount of energy consumed. When adequate information is available, growth can be separated into somatic and gonadal components. More detailed discussions of fish bioenergetics and modeling are available elsewhere (Brett and Groves 1979; Kitchell 1983; Hewett and Johnson 1987; Adams and Breck 1990).

Bioenergetics Model Applications

A major advantage of the bioenergetics modeling approach is that all components of the energy budget must balance. Therefore, if one component is too difficult or expensive to measure directly, it can be estimated from more easily obtained measurements or approximations of the other components. For example, field measurements of food consumption usually require labor-intensive, 24-h sampling and have inherently large measurement error (Cochran and Adelman 1982). With a small amount of data on temperature and

fish size and a bioenergetics model that summarizes the growth process, however, food consumption can be estimated very reliably from growth, which is easily measured (Rice and Cochran 1984). Stewart et al. (1981) used this approach to estimate the predatory impact of stocked salmonids on Lake Michigan alewives *Alosa pseudoharengus* and predicted the alewife decline that has occurred in recent years. Bioenergetics models have also been used to estimate seasonal effects of sea lampreys *Petromyzon marinus* on salmonid populations (Kitchell and Breck 1980), optimal stocking strategies for esocids in Ohio reservoirs (Bevelheimer et al. 1985), temperature effects on growth and condition (Kitchell et al. 1977; Rice et al. 1983), effects of macrophyte harvesting on predator-prey interactions (Breck and Kitchell 1979), life history benefits of diel migration (Caulton 1978), optimal growth of fish in hatcheries (Stauffer 1973), and a variety of other effects (Adams and Breck 1990). Bioenergetics models have been used for many years to study the fate of contaminants in aquatic systems, especially accumulation of contaminants in fish (Norstrom et al. 1976; Weininger 1978). Little work has been done on modeling the effects of contaminants on fish, however (O'Neill et al. 1982; Breck and Bartell 1988).

Generally, bioenergetics models have been based on parameters derived from data on fish assumed to be healthy and unstressed, and they have been used to address questions about fish populations assumed to be healthy and unstressed. Very few models specifically incorporated the effects of stressors on components of the energy budget (e.g., O'Neill et al. 1982; Cuenco et al. 1985a). Yet the bioenergetics modeling approach offers some important advantages for studying stress in fishes. These models mechanistically integrate the multiple factors that affect growth, but they are not overly complex; the equations are fairly simple, and the computer programs used are mostly for "bookkeeping." The daily time step used in most applications gives good temporal resolution for looking at short-term, long-term, and intermittent effects of stress. Models have already been developed for many species, including bluegill *Lepomis macrochirus*, yellow perch *Perca flavescens*, walleye *Stizostedion vitreum*, largemouth bass *Micropterus salmoides*, alewife, and several salmonids (Hewett and Johnson 1987), and thorough sensitivity analyses have been conducted on the models (Kitchell et al. 1977; Stewart et al. 1983;

Bartell et al. 1986). These tests have demonstrated that a model's predictions are generally quite robust, and they show clearly which parameters have the greatest influence on predictions.

Most important, bioenergetics models work well. Tests of a model's predictions are rare for the same reason that the model is applied in the first place: the requisite data are difficult to obtain. But Rice and Cochran (1984) were able to test the predictive power of a model for largemouth bass by means of independent field data on the species' growth, feeding rates, and water temperature. We found that the cumulative food consumption predicted by the model from observed growth and water temperatures was within 8.5% of that estimated directly from field measurements of feeding rate. When growth throughout the season was predicted only on the basis of water temperature, observed food consumption, and initial size of the fish, predicted weights corresponded closely to observed weights, with no significant lack of fit.

Bioenergetic Approaches to Stress

How can bioenergetics modeling be used as a tool in studying the effects of stress on fishes? One approach is to use a "healthy fish" model as a null hypothesis to investigate whether or not observed growth patterns can be explained by environmental factors without invocation of stress effects that alter fish physiology. For example, one can ask whether interactions between prey availability and temperature or body size adequately explain an observed growth pattern, or whether a stressor that affects the energy-budgeting process must be invoked. A second approach is to incorporate into the model known effects of stressors on physiology and simulate the derived effects of these stressors on growth or food consumption. Vaughan et al. (1982) espoused the advantages of this approach, but it has rarely been applied. Cuenco et al. (1985a) developed a bioenergetics model for channel catfish *Ictalurus punctatus* that included dose-dependent functions for the effects of oxygen and un-ionized ammonia concentrations on food consumption. By incorporating these effects, Cuenco et al. were able to examine the interactions among oxygen and ammonia concentrations, fish size, temperature, stocking densities, and feeding rates, and to evaluate the effect of these variables on growth in an aquaculture production system (Cuenco et al. 1985a, 1985b, 1985c). O'Neill et al. (1982, 1983) used bioenergetics modeling to evaluate how predator-prey and competitive interactions modify the expected

direct effects of toxicants in a highly interconnected aquatic system.

In this paper I discuss the potential of bioenergetics modeling as a tool that can further understanding of the effects of stress on fish populations and communities. I use one example from the literature to illustrate how the "null model" approach was successfully applied to a real problem, and I present several examples to demonstrate the power and flexibility of the second approach—incorporation of stress effects directly into the model—for exploring the effects of stress on fishes.

Null Model Approach

Par Pond, a large cooling reservoir in South Carolina, receives heated effluent from a nuclear reactor. For many years, observers have noted a strong seasonal variation in the body condition of largemouth bass in the heated arm of Par Pond; condition declines sharply during the spring and early summer, when some individuals become extremely emaciated, and rises strongly during the fall and winter (Esch et al. 1976; Gibbons et al. 1978; Hazen and Esch 1978; Hazen et al. 1978). Condition of largemouth bass in unheated (ambient-temperature) areas of the reservoir is fairly good throughout the year and shows a moderate peak during the winter.

Several hypotheses have been proposed to explain this "thin-bass" syndrome. One explanation is that the higher metabolic costs caused by elevated water temperatures causes weight loss and lower body condition during the summer (Esch et al. 1976; Gibbons et al. 1978). Giesy (Rice et al. 1983) found high mercury concentrations in tissues of Par Pond largemouth bass; these concentrations were inversely correlated with condition of the fish. Elevated mercury levels may reduce conversion efficiency or appetite in some way, or they may induce a "behavioral fever" response (Reynolds et al. 1976) that causes largemouth bass to seek higher water temperatures. High incidences of *Aeromonas* and *Epistylis* infections or of redsore disease, have been observed in Par Pond largemouth bass, and Esch et al. (1976) found that infected individuals were in worse condition than uninfected fish. Stress caused by the infections may reduce conversion efficiency or feeding rate in the infected fish.

Alternatively, the null hypothesis for the thin-bass syndrome is that the observed condition pattern is simply the natural result of interactions between "normal" largemouth bass physiology

and behavior and prevailing conditions of temperature and food availability in the heated area of Par Pond. We used a bioenergetics model for largemouth bass to determine if this null hypothesis is valid, or if some additional stressor affecting growth must be invoked to explain the thin-bass phenomenon (Rice et al. 1983).

Bioenergetic analysis.—We simulated growth and condition of the average-size Par Pond largemouth bass from both heated and unheated areas. We used largemouth bass body temperatures reported by Bennett (1979) and assumed various constant feeding rates (in grams per day, percentage of body weight per day, or percentage of maximum ration per day) to test the hypothesis that seasonal changes in water temperature alone could account for the observed patterns. The patterns predicted from these simulations did not match the observed patterns in either the heated or unheated areas; this result suggested that temperature effects alone are not responsible for the thin-bass syndrome.

Largemouth bass are typically quite inactive with average swimming speeds around 1–5 cm/s (Rice 1981). Metabolic costs increase exponentially with swimming speed, so changes in activity level, perhaps in response to heated effluent, might contribute to the thin-bass condition. To test this hypothesis, we used observed body temperatures and constant feeding rates in the model and allowed swimming speed to vary as necessary to fit the observed patterns of body condition. The results showed that variable activity is not a likely explanation; largemouth bass would have had to swim continuously at speeds of more than 25 cm/s for several months and at negative speeds for several other months to produce the observed pattern!

Mature female Par Pond largemouth bass lose about 4% of their body weight in reproductive products when they spawn in the spring; thus, spawning might contribute to the decline in condition observed in the summer. We evaluated the influence of spawning by simulating seasonal changes in condition using observed body temperatures, constant levels of food consumption, and a 4% weight loss in the spring. This liberal estimate of weight loss at spawning accounted for only about 20% of the observed decline in condition; spawning may contribute in a minor way to the thin-bass pattern, but is not likely to be the primary cause.

Food availability can vary independently of temperature, so we considered the hypothesis

that seasonal changes in food availability, coupled with observed body temperatures, might account for the seasonal change in body condition. With the model, we found that a strong seasonal variation in food availability, lowest in late winter and spring and highest in late summer through early winter, could account for the observed patterns of body condition when coupled with observed largemouth bass body temperatures. The feeding rates required were reasonable, ranging from 16 to 75% of maximum; similar patterns of food availability could explain the different body condition patterns in the heated and unheated parts of Par Pond (Rice et al. 1983).

Janssen and Giesy (1984) subsequently demonstrated that the thin-bass syndrome is indeed the result of strong seasonal variation in food availability. Blueback herring *Alosa aestivalis*, important prey of Par Pond largemouth bass, aggregate near the heated outfall during the fall and winter to feed on zooplankton in the effluent. Largemouth bass prey heavily on these aggregations. During the rest of the year, blueback herring are limnetic and largely unavailable to largemouth bass. Thin bass tend to stay near the outfall, perhaps because it is the only area where, in their emaciated condition, they can capture prey.

Our bioenergetics analysis of Par Pond largemouth bass used a "healthy fish" model to show that stress effects due to infection, high contaminant concentrations, or high activity levels need not be invoked to explain the thin-bass syndrome. Rather, this phenomenon could be explained by normal energetic constraints imposed by seasonal variation in prey availability interacting with temperature. With a null model, we eliminated several less parsimonious explanations and identified a likely, testable hypothesis that was not readily apparent from the observed growth pattern.

Direct Approach

Stress effects can be directly evaluated with a bioenergetics approach if the physiological consequences of a stressor can be included mechanistically in the model. Stressors can affect every component of the energy budget. Many of these effects are already known (Schreck 1990; Thomas 1990; both this volume). Exposure to toxicants such as copper, pentachlorophenol (PCP), crude oil, and other compounds can substantially reduce a fish's appetite and food consumption, which subsequently affects growth (Lett et al. 1976; Brown et al. 1987; Heath 1987; Kiceniuk and Khan 1987). Behavioral changes induced by stress-

ors may also affect feeding rate. Brown et al. (1987) showed that exposure to PCP not only reduced the number of feeding attempts by young-of-the-year largemouth bass, but also reduced their efficiency at capturing prey.

Some stressors such as physical disturbance and some chemicals substantially increase metabolic rate (Webb and Brett 1973; Smart 1981; Barton and Schreck 1987). Others such as organophosphates may have narcotic effects that reduce metabolism (Heath 1987). Depressed metabolic rates have also been found in fish exposed to copper, mercury (Hughes 1976), and chlorine (Bass et al. 1977) and are due to gill damage and excessive mucus production. Individual stressors may affect metabolism very differently according to the intensity of exposure. Anderson (1971) found that low concentrations of DDT decreased the respiration rate of Atlantic salmon *Salmo salar*, but high doses increased it.

Stressors may indirectly affect metabolic costs by increasing or decreasing a fish's activity level. For example, zinc, cadmium, and chromium all increase spontaneous activity of bluegills up to over 700% in a dose-dependent manner (Ellgaard et al. 1978). Respiration rate may also be affected indirectly by stressors that change a fish's preferred temperature. Reynolds et al. (1976) suggested that fish may have evolved a "behavioral fever" response to fight natural stresses such as diseases. A variety of toxic chemicals and diseases affect preferred temperature (e.g., Ogilvie and Anderson 1965; Reynolds and Covert 1977; Domanik and Zar 1978), and changes of $\pm 4^\circ\text{C}$ are not uncommon (Peterson 1976). These changes can have a substantial effect on metabolic rate; Muchlinski (1985) found that the 4.8°C increase in preferred temperature of goldfish *Carassius auratus* caused by the bacterium *Aeromonas hydrophila* (Reynolds and Covert 1977) increased metabolic cost 64.5%.

Little is known about the effects of stress on food assimilation by fishes, but it seems plausible that some stressors may reduce the efficiency of digestion or assimilation processes. Parasites reduce the energy available to their host for growth; they may be treated as an energy "sink," or their effects may be modeled as reduced assimilation efficiency.

Stress effects on components of the energy budget may be manifested in a dose-dependent fashion, and they may be continuous or intermittent in their influence. Variables like temperature or body size can interact with stressors to moder-

ate or exacerbate the stress effect. Effects of multiple stressors may be additive, compensatory, or depensatory. When the mechanism by which a stressor affects the allocation of energy is known, it can be incorporated into a bioenergetics model and used to evaluate the potential consequences of that stressor in a variety of situations. Some stressors, such as toxicants, can be grouped according to their mode of action (McKim et al. 1987a, 1987b); such a grouping may simplify model implementation.

Bioenergetic Simulations of Stress Effects

I will use a series of simulations with the same largemouth bass model applied to the Par Pond problem (Rice et al. 1983) to demonstrate the power and flexibility of the bioenergetics modeling approach for evaluating stress, and also to reveal some implications of known stress effects that might not otherwise be obvious. Each stress-effect simulation incorporated the following conditions: (1) simulations ran from April 1 through late November; (2) the thermal regime approximated that of a typical southern reservoir, in which temperatures follow a sine curve peaking at 31.5°C at the end of July and dropping to 5°C at the end of January; (3) simulations started with a largemouth bass of 100 g that fed at 50% of its maximum ration throughout the season, a liberal but reasonable rate for fish in the field (Rice and Cochran 1984); (4) except where noted, the largemouth bass thermoregulated at its preferred temperature, staying at 27.5°C whenever surface water temperatures exceeded 27.5°C. Under these baseline conditions, a 100-g largemouth bass reached 419 g by the end of a simulation. Because growth represents surplus energy remaining after all other demands on the energy budget have been met, stress has a proportionately greater effect on animals that grow slowly. Largemouth bass growth in the baseline simulation was fairly fast, so any stress effects demonstrated in the following simulations are likely to be conservative.

Effects on Feeding Rate

Appetite depression is a common response of fish to stress. Cessation of feeding for long periods obviously has a large effect on growth, but how important might smaller, chronic decreases in feeding rate be? Simulations with the largemouth bass model showed that a 20% reduction in feeding rate (from 0.5 to 0.4 maximum ration) throughout the season—due to the stress of a toxicant, for example—reduced net growth by 64%. When

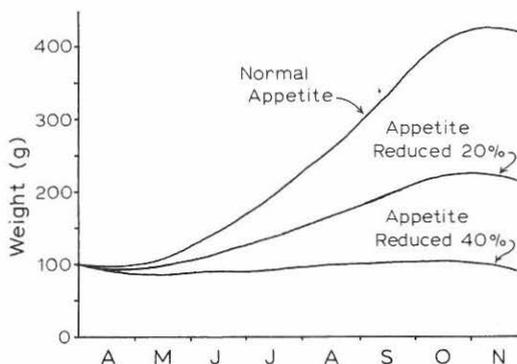


FIGURE 1.—Simulated growth patterns, early April to late November, for a 100-g largemouth bass feeding at a "normal" rate (0.5 maximum ration) and at rates 20 and 40% below normal.

feeding rate was reduced by 40% (to 0.3 maximum ration) net growth was slightly negative (Figure 1). Vaughan et al. (1982) did a similar analysis for a Lake Michigan coho salmon *Oncorhynchus kisutch*, which would typically grow from 30 g to 4 kg over 2 years. They found that if feeding rate was reduced about 25%, net growth declined by 50%; when feeding rate was reduced about 40%, net growth dropped by 75%. Although chronic appetite depression may not have short-term effects on survival, even low levels of depression can have a substantial effect on growth, which has implications for reproduction, predation, and other size-dependent processes. Effects of varying stress levels on feeding rate can be simulated by incorporation of a dose-dependent function directly into the model, as was done by Cuenco et al. (1985a) to investigate the effects of oxygen and un-ionized ammonia concentrations on channel catfish feeding rates. Within certain bounds, feeding rate declined linearly with declining oxygen concentration or increasing ammonia concentration, and the effects on growth rate were substantial. For example, when oxygen declined from 7 to 5 mg/L, the growth rate of a 10-g channel catfish at 28°C was halved from 7 to just over 3%/d (Cuenco et al. 1985a).

Some stressors can also cause transient appetite depression. For example, rainbow trout *Oncorhynchus mykiss* stopped feeding when exposed to copper concentrations of 0.1–0.3 mg/L, but their appetite gradually returned to normal over 5–15 d depending on the dose (Lett et al. 1976). Could a single event like this have a significant effect on growth? I simulated such an event for largemouth bass by reducing food consumption to

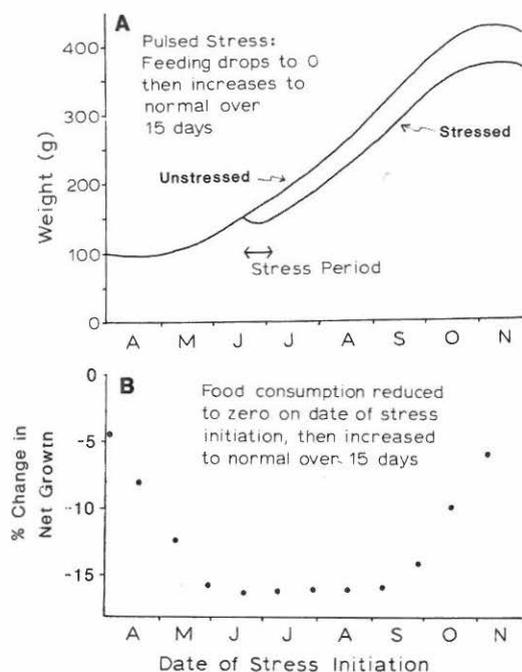


FIGURE 2.—(A) Simulated growth patterns for an unstressed 100-g largemouth bass feeding at 0.5 maximum ration throughout April–November and for a stressed fish whose appetite dropped to zero in mid-June then gradually increased to normal over 15 d. (B) Magnitude of change in net growth for 12 largemouth bass simulations, each including a single, transient reduction in appetite (as in A), initiated at a different point in the season.

zero in mid-June, then gradually increasing it to normal over 15 d. This single, transient, stress effect caused a 16.3% reduction in net growth over the whole season (Figure 2A); I assumed that no compensatory increase in feeding rate occurred afterward. Because size and temperature both affect feeding rate, the magnitude of this growth reduction varied from 4.5 to 16.3% according to when during the season the stress period occurred (Figure 2B); the largest effect occurred during the summer months.

Effects on Metabolic Rate

Relatively small chronic increases in respiration rate can have large effects on growth similar to those caused by reduced appetite. A 10% increase in metabolic rate reduced net growth in the largemouth bass simulation by 22%, and a 20% increase caused a reduction of 42% in net growth. Vaughan et al. (1982) found that similar increases in respiration rate had smaller effects on coho

salmon growth; growth was reduced by only 8 and 16%, respectively. Differences in feeding and growth rates may explain why this stress had a smaller effect on coho salmon than on largemouth bass. The coho salmon simulation required higher feeding rates (0.63–0.74 maximum consumption) than the largemouth bass simulation to produce the higher growth rates observed for coho salmon; the hierarchy of energy allocation dictates that fish with lower energy intakes and growth rates have proportionately greater responses to a stressor. The effect on largemouth bass growth may also have been more pronounced because of the warmer temperatures used in the simulation. These simulations illustrate the effects of increased metabolism; some stressors decrease metabolic rate, but reduced feeding probably also occurs, so growth would not be enhanced.

Metabolic rate may be affected indirectly by stressors that change the preferred temperature of a fish. In previous simulations, the largemouth bass thermoregulated behaviorally to stay at the preferred temperature of 27.5°C when surface waters exceeded that temperature. How might growth respond to a 4°C increase in preferred temperature, as might be induced by DDT (Olgivie and Anderson 1965) or *Aeromonas* (Reynolds and Covert 1977)? To simulate this response, I allowed the largemouth bass to remain in surface waters at temperatures up to 31.5°C through the summer. These higher temperatures increased metabolic rate and decreased food consumption, resulting in a 29% decrease in net growth over the season (Figure 3). A similar effect might be expected when fish are forced to occupy waters that exceed their preferred temperature because cooler waters are anoxic or simply not available (Coutant 1985).

Effects of Intermittent Stress

Stressors of large magnitude or long duration, even if they have low intensity, can have substantial effects on growth, but the consequences of brief, intermittent stress are not as obvious. It is not atypical for fish to cease eating for a day or so after they are handled, and handling can also cause transient increases in metabolic rate. Respiration rates of juvenile steelhead *Oncorhynchus mykiss* were more than double normal rates 1 h after several brief (2-min) disturbances (Barton and Schreck 1987), and the stress of passing through a size-grader increased the oxygen consumption of rainbow trout 50–60% for 1–2 d (Smart 1981). Repeated electroshocking can re-

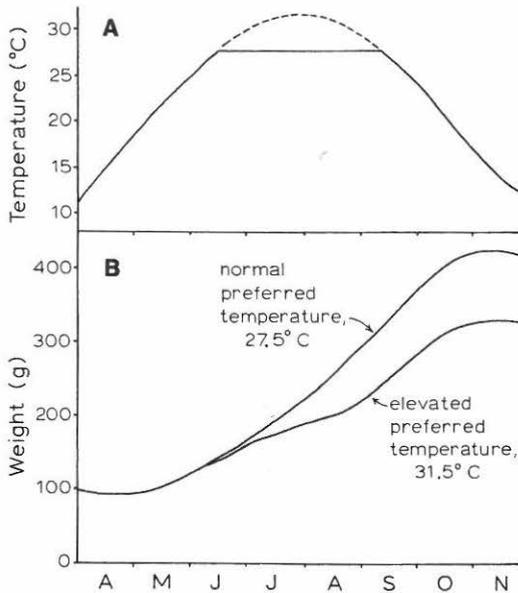


FIGURE 3.—(A) Simulated temperatures experienced by largemouth bass with a normal preferred temperature of 27.5°C (solid line) and by fish with a stress-elevated preferred temperature of 31.5°C (dashed line). (B) Simulated growth of largemouth bass with normal and elevated preferred temperatures.

duce the growth rate of fishes (Gatz et al. 1986; Gatz and Adams 1987), primarily because fish cease eating for several days afterward. How significant might the effect on growth be for brief, infrequent stress due to handling or electroshocking? To evaluate this effect, I simulated largemouth bass growth when food consumption was reduced to zero and respiration rate was increased 50% for 1 d every 3 weeks. The cumulative effect of these individual stress events was a 23% reduction in net growth over the season (Figure 4), comparable to that observed by Gatz and Adams (1987) for hybrid sunfish shocked at 2- to 4-week intervals for 3 months.

The substantial growth reduction caused by even infrequent handling or stress has implications for both aquaculture and research. For example, many aquaculturists periodically grade fish to maintain uniform size distributions and increase feeding efficiency. The potential negative effects on growth of such handling may warrant reevaluation of grading methods and frequency. When growth is an important response variable in a research study, it is likely to be measured frequently; in the process, the response of interest may be masked or distorted.

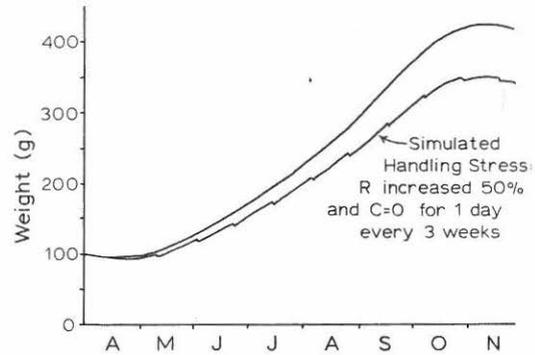


FIGURE 4.—Simulated growth pattern for an unstressed largemouth bass feeding at 0.5 maximum ration and for a fish under the same conditions but experiencing handling or electroshocking stress at 3-week intervals, at which time respiration rate (R) increases 50% for 1 d and food consumption (C) is reduced to zero for 1 d.

Indirect Effects on Ecosystems

Effects of stress at one trophic level may be indirectly manifested at other trophic levels because changes in feeding rate or biomass of individuals in one population may affect the growth or survival of their predators or prey. Direct stress effects on prey species can indirectly increase or decrease the food available to predators. Aerial spraying of pesticides can reduce the biomass of insects in a stream and thus the food available to fish (Elson 1967; Keenleyside 1967). Heat-shocked blueback herring and bluegills entering Par Pond in the thermal discharge provided easy prey for largemouth bass (Janssen and Giesy 1984), and Atlantic salmon *Salmo salar* parr became more susceptible to brook trout *Salvelinus fontinalis* predation after 24 h of exposure to a 1.0-mg/L concentration of an organophosphate pesticide (Hatfield and Anderson 1972). The effects of stress on these trophic interactions often are not intuitively obvious.

As a simple illustration of these indirect effects, I modeled the predation by a 100-g largemouth bass feeding on small bluegills and coupled this simulation with a bluegill bioenergetics model (Breck and Kitchell 1979) to estimate how a 20% reduction in the predator's feeding rate would affect the invertebrate prey eaten by the bluegills. For simplicity, all bluegills started at 1 g (about 40 mm total length) and grew to just over 5 g (about 68 mm) during the simulation, and the largemouth bass fed only on these bluegills. At its normal feeding rate (0.5 maximum ration) the largemouth bass consumed 449 bluegills (1,198 g). When the

largemouth bass's feeding rate was reduced 20% to 0.4 maximum ration, only 287 bluegills (726 g) were consumed, a decline of 39% in total consumption. This magnified effect occurred because the reduction in feeding rate, which is expressed in percent body weight per day, was compounded by lower body weights throughout the season; at the reduced feeding rate, the largemouth bass grew to only 215 g instead of 419 g. The 449 bluegills consumed by the largemouth bass feeding at 0.5 maximum ration had themselves eaten 5,264 g of invertebrates over the season, whereas the 287 bluegills consumed by the largemouth bass feeding at 0.4 maximum ration, plus the 162 additional survivors, consumed 5,810 g over the season. Therefore the 39% reduction in consumption of bluegills by largemouth bass resulted in only a 10% increase in predation mortality for the invertebrate population. The increase in predation on the invertebrate population was relatively small because bluegills that survived until late in the season, when much of the largemouth bass predation occurs, had already eaten nearly as many invertebrates as bluegills that survived the whole season.

This simplistic example does not reflect the true complexity of a natural system, nor does it include the effects of compensatory or depensatory mechanisms and other population-level interactions that would influence the outcome. The effect of changes in largemouth bass predation on a bluegill population would depend greatly on the proportion of the total bluegill population consumed by largemouth bass; if the percentage consumed were low, even a large change in largemouth bass consumption would have little effect, and vice versa. But this illustration does show that stress acting at one trophic level can be manifested at other levels, and demonstrates the potential nonlinearity of effects cascading through a system. O'Neill et al. (1983) presented a much more elaborate bioenergetic analysis that illustrates the importance of these indirect effects (Breck and Bartell 1988; Bartell 1990, this volume).

Discussion

Bioenergetics modeling is a versatile approach with many advantages for studying stress effects on fishes (Table 1). These models can incorporate chronic or transient stress effects, multiple effects and interactions, and indirect effects. The necessity for invoking stress effects can be evaluated with a "healthy fish" null model. When the influence of a particular stressor on the energy budget is understood well enough to incorporate that

TABLE 1.—Advantages and limitations of the bioenergetics modeling approach for studying effects of stress on fishes.

Advantages of bioenergetics models
Can mechanistically integrate all factors affecting growth; can separate stress effects from effects of body size, temperature, and food availability
Can operate at the level of the individual, and can be extended to cohort or population levels
Can be used to investigate long-term or short-term stress effects
Can incorporate chronic or intermittent stress effects, multiple effects, and indirect (trophic-level) effects
Can operate with a temporal resolution (1 d) comparable to laboratory experiments
Can be used to forecast magnitude and direction of future effects and thus to reduce demand for empirical data
Cost effective; can reduce the number of animals required for experiments and alleviate problems caused by inadequate sample size or biased samples
Already available for many species; thorough sensitivity analyses have been done, and model predictions are usually robust
Limitations of bioenergetics models
Substantial numbers of species-specific physiological data are needed to implement a model
Appropriate field data for validating model predictions are very rare
Require specific information (for direct approach only) on how a stressor affects the energy-budgeting process, and how multiple stressors interact (e.g., additively or multiplicatively)
Available data on stress effects are often not in a form readily adaptable to bioenergetics models
Additional research needed on how to incorporate measured stress effects at various biochemical and physiological levels directly into models

mechanistic relationship into a model, the approach becomes even more powerful. Even when we cannot be confident in the exact magnitude of the effect a stressor will have, comparisons of simulations involving stressed and unstressed fish can reveal valuable insights.

Because bioenergetics models operate at the level of the individual, they can address some matters that population-level models cannot, such as how to estimate rates of contaminant accumulation in fishes or to separate the influence of body size from stress effects. In addition, these models can be extended to the cohort or population level (e.g., Stewart et al. 1981; Hewett and Johnson 1987). Mortality and reproduction are size-dependent, so these processes can be indirectly-affected by stress effects on growth rates of individuals. Even low-level chronic stresses may have substantial growth-mediated effects on population size and structure. Coupled with other models, the bioenergetics modeling approach can be incorporated into community or ecosystem analyses to

identify even higher-order effects of stress in aquatic systems (O'Neill et al. 1983; Bartell 1990).

The strengths of bioenergetics modeling are accompanied by some constraints (Table 1). A substantial number of physiological data are needed to fully implement a model, and opportunities to validate predictions with field data are rare (Rice and Cochran 1984). Assumptions can be made from observations on other species when necessary, but varying environmental conditions and even variance in estimates of species-specific parameters add some uncertainty to growth estimates. Fortunately, many of these uncertainties have little effect on model predictions (Kitchell et al. 1977; Rice and Cochran 1984; Bartell et al. 1986). For active fish, assumptions regarding activity level can be important (Stewart et al. 1983), and feeding-rate estimates can have a big effect on predictions of growth (Kitchell et al. 1977). As with any modeling application, the specificity of hypotheses tested or conclusions drawn should be consistent with the model's level of resolution. In many cases, differences between simulations of effects on stressed and unstressed fish may be very robust even when our confidence in exact model predictions is low.

Vaughan et al. (1984) evaluated the utilities of five modeling approaches for quantifying the effects of stress on fish. Surplus-production and stock-recruitment models require long time-series of data, their temporal resolution is coarse, and two or more of the three key processes affected by stress—growth, mortality, and reproduction—are confounded or otherwise cannot be addressed. In yield-per-recruit models, reproduction and mortality are confounded and the temporal scale is coarse. Leslie matrix models require more data and still have coarse temporal resolution, but they can address all three key processes and offer a powerful approach to some problems. Bioenergetics models require the most detailed data, but can address all three key processes with daily temporal resolution, which is the time scale most comparable to laboratory studies of stress effects. They operate at the level of the individual, can be used to analyze responses to multiple stresses, and provide the only approach that mechanistically links stress effects with the growth response.

Bioenergetics modeling can serve as a short-term indicator of the effects of long-term stress. The effects of some stressors, particularly chronic or low-level ones, may be difficult to detect empirically over short time periods. For example, indirect effects of stress on population abundance

or size structure may only become apparent after several years, and monitoring such effects over long time periods may be difficult or impossible. Bioenergetics modeling can be used retrospectively to decipher what may have happened in a system, but one of its most valuable applications is in forecasting the potential magnitude and direction of future effects. This kind of analysis can reduce the amount of empirical data needed by identifying the subset of key observations required to detect an effect, and it can help estimate potential costs and risks in advance.

These attributes make bioenergetics modeling a cost-effective approach to evaluating stress effects on fishes in a variety of applications. Aquaculture producers are continually seeking ways to optimize production and maximize the efficiency and profitability of their operations. The high feeding rates and stocking densities that are necessary to achieve economical production levels also increase the potential for stress, which can reduce growth and increase mortality. Models that incorporate stress effects on growth (e.g., Cuenco et al. 1985a, 1985b, 1985c) in combination with the economic implications of management alternatives can be used to evaluate various scenarios and optimize production strategies (Knights 1985).

Regulatory agencies and private industries are spending enormous amounts of money to evaluate the potential effects of toxicants on aquatic systems. Yet the proliferation of manufactured compounds has far outstripped our empirical testing capabilities, even for straightforward, acute effects that lack ecological realism. Responses to stress can vary substantially with the size, developmental stage, or reproductive condition of fish, with water temperature, and with other variables such as food availability. Adequate resources are not available to evaluate all the major combinations of environmental factors and toxicants that can cause stress, especially long-term stress. Bioenergetics models can separate the effects of stress from those of allometry, temperature, and food availability, and can allow quantitative comparisons between laboratory experiments performed with different species or sizes of fish under different conditions without confounding the results. This partitioning of effects can also help with extrapolations of laboratory results to other environmental conditions for impact assessment. Efforts to classify chemicals according to their mode of action in fishes (McKim 1987a, 1987b) and to group species according to their sensitivities

(Neuhold 1987) could further facilitate application of the bioenergetics approach by linking certain stress responses to whole groups of toxicants or species. If we focus laboratory studies on determining how stressors affect the major components of the energy budget, we can integrate these results into bioenergetics models to more efficiently evaluate potential effects and interactions and even to estimate some effects that could not be measured directly.

Bioenergetics modeling can alleviate some of the problems associated with inadequate or biased samples. It often is difficult to collect enough fish of appropriate size and sex for growth analyses. Field sampling is time-consuming and costly. Destructive sampling exacerbates the problem. Selective collection techniques or size-dependent effects on growth and mortality can bias estimates for individuals or populations. In many cases, model simulations can provide the same information much more efficiently and bypass these sampling constraints.

Growing constraints on the use of live animals in experimentation also enhance the value of modeling. In Great Britain, for example, any procedure inflicting pain, suffering, distress, or lasting harm (specifically including physiological stress) on a vertebrate animal can be carried out only by an individual licensed to conduct that particular procedure on a specific type of animal at a specified facility in association with a specified and licensed project (Cooper 1987). License applications are closely scrutinized to evaluate the necessity of a particular treatment relative to less severe alternatives. Many restrictions on the use of live animals apply to fishes, and these limitations are likely to become an increasingly important factor in both laboratory and field studies (ASIH et al. 1988). Bioenergetics modeling offers a way to get more information from fewer experiments and to reduce both the number of animals used and the cost of using them.

Historically, bioenergetics models have not been developed in the context of research on stress, but adequate background studies have been done to make such models useful for evaluating the effects of stress on fish at the individual and even the population level. Bioenergetics models are already available for more than 30 species of fish (Vaughan et al. 1982; Hewett and Johnson 1987). Hewett and Johnson (1987, 1989) developed a general fish bioenergetics modeling program that synthesizes many of these previous modeling efforts. The menu-driven program con-

tains complete models for 11 different species and has options that allow one to easily adapt it to other species. Users can also simulate multiple cohorts, different mortality rates, changing diet composition or caloric density, and varying food availability. These advances have made bioenergetics modeling a readily available tool that can substantially enhance our understanding of the consequences of stress on fishes.

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