USE OF A COMPUTER MODEL TO DETERMINE ENERGY REQUIREMENTS OF A PREDATORY FISH, THE LARGEMOUTH BLACK BASS (MICROPTERUS SALMOIDES)

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ABSTRACT

In some types of biological research the techniques of engineering and other applied sciences have figured prominently in many significant advances made during the last ten years. Such analytical methods as simulation studies, optimization techniques, dynamic programming, and others have opened whole new theoretical and mission-oriented capabilities in many areas of investigation. The analysis of energy flow in both individual animals and populations of animals has been one field of ecological research that has developed rapidly, and one which will continue to enlarge in scope in the future. However, modern numerical techniques are not solely responsible for advances in energetics analysis. Rather, progress has been due to the conceptual framework for study that has developed from principles and considerations underlying theory in many seemingly diverse disciplines. At first glance, such areas of endeavor as urban transit system design, land and resource management strategies, urban planning, and economic theory do not appear to be too closely related. However, all of these activities along with the study of energetics in ecological systems have in common the analysis and optimization of energy flow.

In economics, for example, one necessary desideratum is cash flow. In ecology, calories are the currency and energy debits, and credits must balance or show a net surplus for every organism if it is to survive. The environmental prerequisites which must be met before a business will flourish are essentially the same in principle as those dictating the survival of animals in nature. Such considerations as food density, habitat complexity, competition, and basal metabolic requirements are key features in the analysis of energy flow in ecological processes and have analogs in many areas of interest, economics being but one example.

Among ecological studies, the process of predation is one which has attracted the attention and energies of biologists for many years. Generally, the predatory process is studied from the viewpoint of time spent by the predator in various activities such as searching for, pursuing, or capturing prey organisms. While the time that a predator devotes to different aspects of living is important, time itself is only an indirect measure of that most critical of commodities which all organisms must obtain from their environments--energy. Measures of time may be of direct value for some determinations of population dynamics, but time actually serves only as a rough index to the relative rates of energy acquisition and dissipation of individual predators. It is not time *per se* which determines the success or failure of a predator, but rather optimization of the balance which must be struck between rates of energy acquisition and expenditure. An analysis of predator energy requirements was employed to explore some aspects of a problem in predation which arises from an apparent discrepancy between predator-prey relationships in nature and corresponding laboratory systems. The disparity between these two situations can be summed up as follows. In nature most predators and their prey coexist in the same general environment for indefinite periods of time without either the annihilation of the prey by a predator or prey populations becoming so abundant because of inefficient predators that habitat resources are depleted. Conversely, in the laboratory prey abundance generally oscillates wildly with decimation or complete extinction of prey animals and subsequent starvation of predators as the usual outcome.

One key feature of natural environments which does not obtain in the laboratory is the presence of refuges for prey. Refuges may be of many different types, but in general they can be classified into two main categories. A refuge may be wholly restrictive to the predator--the predator may be physically unable to penetrate certain areas of the habitat, thereby allowing prey to escape. On the other hand, a refuge may be only partially restrictive to the predator, due to some behavioral characteristic or because speed and/or maneuverability of the predator is hindered.

Laboratory experiments of three main types were performed to provide raw data for an energetics analysis of a predator. The predator selected for study was the largemouth black bass (*Micropterus salmoides*) since this fish is a well-known and voracious predator. The first series of laboratory experiments were designed to yield data which could be used to develop a mathematical and computer model of the routine metabolic requirements of largemouth black bass. Routine metabolism was further subdivided into standard or basal metabolism and the specific dynamic action of food (SDA). Figure 1 shows a graphical

representation of the hypersurface of the model of these two components. A hypersurface is shown since this is a more comprehensible and complete portrayal of the model characteristics than either single variable regression lines or families of curves. Table I gives the results of a test to determine the sensitivity of model components to perturbations in parameter and variate values.

Active metabolism experiments designed to reveal the effect of swimming velocity on energy requirements were then performed. The resulting data were formulated into a model of active metabolism which was in turn incorporated into the model for routine metabolism. The energetics model which resulted from this combination was then used to explore some implications and consequences of environmental complexity on the process of predation. To do this, approximately 50,000 frames of movie film taken of feeding sessions were analyzed individually. By incorporating the model of energy requirements into an analysis of film records, it was possible to determine the energetic consequences of predation by largemouth black bass in environments with varying degrees of cover density.

It was tentatively concluded that predatory success in terms of long-term survival, and probably prey survival as well, would occur at levels of cover density intermediate between a completely unobstructed environment (no refuges for prey) and one in which the cover density was high (370 units/m^2). The optimality of intermediate cover densities was based in part upon energetic considerations. It was found (not unexpectedly) that energy input to the predator was maximal when the feeding area was completely unobstructed. However, it is well known that in simple laboratory environments prey are generally exterminated which results in starvation of the predator. Therefore, lack of refuges for prey was considered to be suboptimal for both prey and predators. High cover densities, on the other hand, necessitated higher velocities at capture by the predator which in turn caused a disproportionately high rate of energy utilization. This, together with a decrease in maneuverability of the predator and an increase in the capability of prey to escape, gave rise to the conclusion that high cover densities as well as low cover densities were suboptimal.

The efficiency of energy utilization by the predator was measured by means of two indices. The first was work accomplished per milligram oxygen consumed at each cover density at the time of capture. The second index used as a measure of efficiency of energy utilization the centimeters travelled per milligram oxygen consumed at each cover density at the time of capture. Table II shows, in the last two columns, the numerical values for these two indices at four levels of environmental complexity. It is readily seen that work per milligram oxygen consumed remains relatively stable until the highest cover density; in addition the column headed centimeters travelled per milligram oxygen consumed declines more and more abruptly with an increase in cover density. It is obvious that both indices are derived from movement and that cover density will ultimately become so high that the bass simply cannot penetrate it. At that point both indices equal zero, and the refuge becomes qualitatively different (totally restrictive to the predator). It was therefore concluded that for long-term predator survival a balance between energy acquisition and energy dissipation could be achieved at intermediate levels of environmental complexity (cover density).

FIG. 1. SURFACE REPRESENTATION OF ROUTINE METABOLISM MODEL.
EACH SURFACE REPRESENTS A TIME DEPRIVED, TIME DEPRIVED IS IN DAYS.

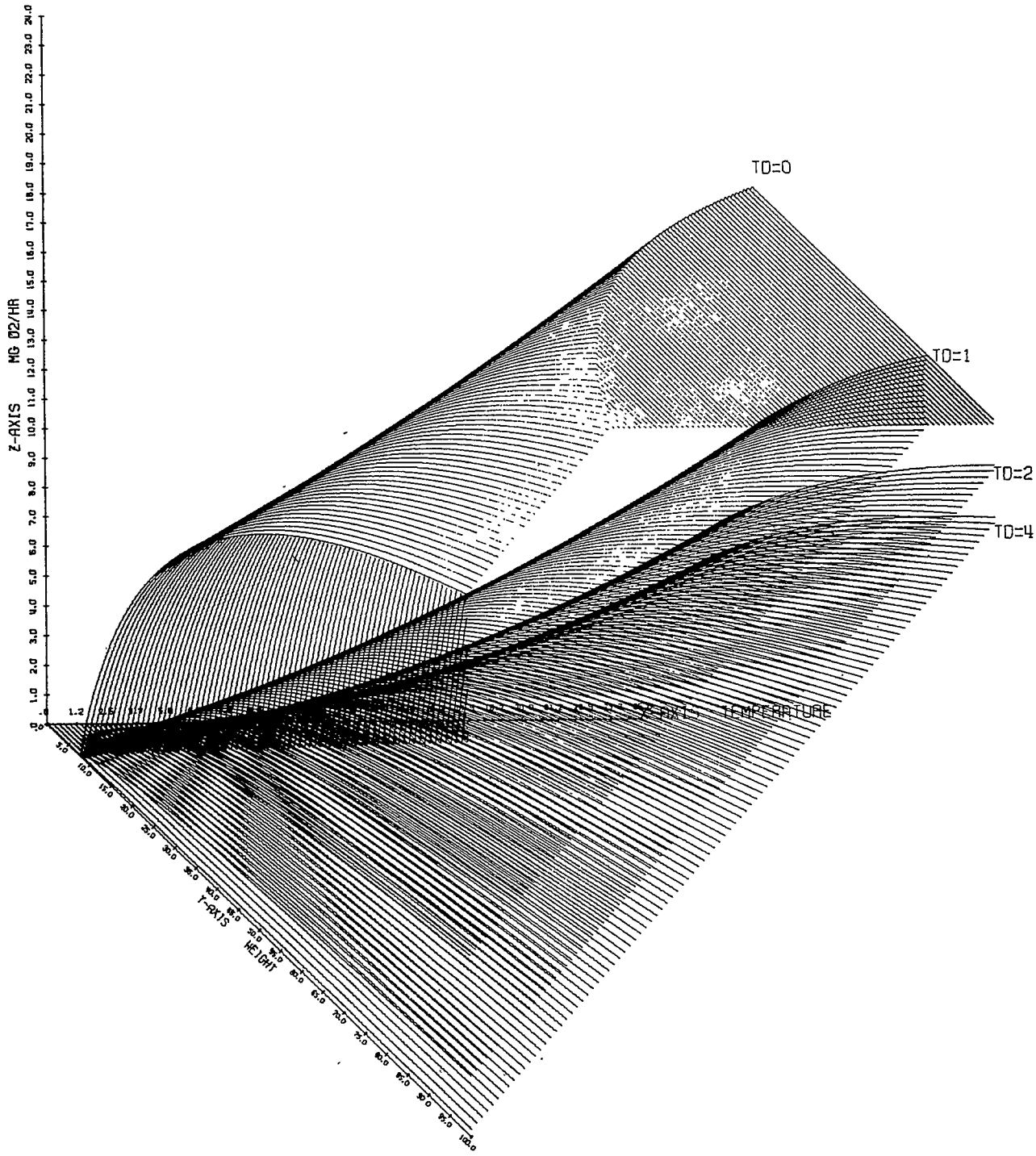

Table I. Results of the sensitivity test of the computer model (equation (13)) at 20°C for an arbitrarily selected weight of 50g and TD of 0.5. Each variable or constant was varied individually and the resulting percent change in routing oxygen consumption appears in the matrix.

% deviation	Constant or variable							
	a	b	b′	a′	c	T	W	TD
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10	6.03	17.15	8.30	-4.33	-2.13	6.03	5.81	-2.13
20	12.05	39.17	16.61	-8.66	-4.14	12.05	11.33	-4.14
30	18.08	67.46	24.91	-12.99	-6.04	18.08	16.59	-6.04
40	24.11	103.80	33.22	-17.32	-7.85	24.11	21.62	-7.85
50	30.13	150.48	41.52	-21.65	-9.55	30.13	26.46	-9.55
60	36.16	210.43	49.82	-25.98	-11.17	36.16	31.13	-11.17
70	42.19	287.45	58.13	-30.32	-12.70	42.19	35.64	-12.70
80	48.21	386.37	66.43	-34.65	-14.14	48.21	40.00	-14.14
90	54.24	513.44	74.74	-38.98	-15.51	54.24	44.24	-15.51
100	60.27	676.67	83.04	-43.31	-16.81	60.27	48.36	-16.81

Table II. Level of significance, using Student's t-test, of the difference between mean velocity at attempt and mean velocity at capture for each cover type. In parentheses are degrees of freedom. Columns 5 and 6 were determined from equations (14) and (14a).

Cover type	Av. velocity at attempt (cm/sec)	Av. velocity at capture (cm/sec)	Level of significance	Work/mg O_2 1/ at capture (g-cm/mg O_2)	Cm traveled/mg O_2 2/ at capture
1 (6)	57.01	23.68	.001	2.67	0.642
2 (4)	51.35	23.12	.01	2.62	0.630
3 (4)	57.01	50.12	.1	2.72	0.480
4 (6)	42.29	69.59	.01	2.44	0.194

1/ Numbers in this column should be multiplied by 10^5.

2/ Numbers in this column should be multiplied by 10^4.