

INTERNAL REPORT 36

TROPHIC RELATION MODEL IN AQUATIC COMMUNITIES SOCKEYE SALMON MODEL, WOOD RIVER LAKES, ALASKA

Douglas M. Eggers and Donald E. Rogers

University of Washington

The objective of this study is to develop a mathematical model to relate the production of juvenile sockeye salmon in the Wood River Lake system to parent stock size, primary and secondary production, population size of predators and competitors, and abiotic variables.

METHODS AND PROCEDURES

Data exist for the Wood River Lakes system (Bristol Bay, Alaska) from 1958 to 1970. These have been consolidated and classified into those variables deemed necessary to substantiate a trophic dynamic model of the system. Most effort has been spent looking at suspected linear relations, employing correlation, regression, and analysis of variance techniques.

More data exist for Lake Aleknagik than for the other lakes in the system (Nerka, Little Togiak, Beverley, Kulik). The planned approach was to fit the model to the Aleknagik data first and then generalize to fit the other lakes in the system. There are differences among the lakes in climate, productivity, spawning, abundance of predators, and competitors. The ability in the model to compensate for these differences will, in effect, prove the validity of the model.

We have formulated a compartmentalized version of the model, without any pathway equations. We have divided the lake into two zones, the limnetic zone and the littoral zone. Different biological relations occur in them and will have to be included in the model. These zones are somewhat independent, except that sockeye salmon and sticklebacks move between them seasonally.

Although most pathway equations must be formulated, some preliminary equations have been determined. These, a result of literature search, relate phytoplankton and zooplankton interaction in the limnetic zone of the lake. This model was determined by G. A. Riley in the 1940's. It is basically an extended type of predator-prey model. The abiotic variables, solar radiation, nutrients, and turbulence have been included. The Riley model is presented later in this report.

We have little information about the Wood River system from October through May. To model the system during the winter will be difficult. Our approach is to assume some simple submodel that reflects the believed relations. By incorporating this into the overall model and systematically looking at various parameter combinations and how they affect production, we can pin down the exact formulation.

FORM AND UNITS OF DATA

The data are primarily in metric system units of biomass and numbers of organisms. Because the volume and surface area of the lakes are known, these can be transformed easily into density units.

Type and amount of data available are given in Table 1. Only those measurements made over a period that exceeds 6 years are listed. Measurements of oxygen, total dissolved solids, and mineral content of lake water were made in 1961-1962. The food habits of dominant fish species in the lake system have been determined in 1-3 years. Density of benthic organisms was measured throughout the lake system in 1965, and the abundance of emergent aquatic insects has been measured for 2 years in Lake Aleknagik.

The values for 26 of the variables that we believe are most important are given for Lake Aleknagik in Table 2. Population estimates are based on catch per unit effort of sockeye and sticklebacks and are supplemented by echo-sounding data (Rogers 1967).

Parent egg deposit is calculated from the lake system escapement enumeration and aerial spawning ground surveys conducted by the Alaska Department of Fish and Game, in addition to smaller surveys conducted on foot (Gilbert 1968).

Biomass is simply the product of average weight and population size. Growth rates are based on a simple exponential model:

$$W_t = W_0 e^{at},$$

where

t = time,

W_t = weight at time t ,

W_0 = initial weight, and

a = growth rate.

For each year, we have a series of length measurements throughout the summer from beach seine and tow net catches. With a fitted length-weight relation and standard regression technique, the parameters W_0 and a were estimated. Climatological observations, water temperature, and lake level are summarized by Rogers et al. (1970).

Zooplankton densities are based on counts of standard plankton net hauls with a 1/2 m net of number-6 mesh. Chlorophyll analysis of filtered algae dissolved in acetone is determined after the model of Richards and Thompson (1952).

RESULTS

During the past year, we have sorted and assembled the data that we think pertinent to a trophic dynamic mode. After the data were gathered together, they were analyzed for statistically significant relations. The data were found to be variable, and seemingly with little apparent linear relations.

The foremost questions that one must consider are: Was this variability because nonlinear relations held, or were our sampling procedures inadequate to estimate the true values of the parameters? Or was there some complex, unknown interaction or random abiotic influence that caused trophic-related population levels to fluctuate independently of each other?

Our statistical analysis and concurrent literature search have yielded some promising results. We have begun to answer a few of the above questions.

Typically, in the Wood River system the phytoplankton population peaks in the spring. Then the zooplankton population peaks. The phytoplankton peak occurs usually in July. After a lag of 2 months, the zooplankton population peak occurs in September. These relations are evident in Table 3. Cyclops scutifer is the predominant zooplankton organism.

The level of phytoplankton and zooplankton population varies from year to year, but the pattern of population changes with the single peak, which occurs each year.

Gordon A. Riley (1946, 1947a, 1947b), Riley and Bumpus (1946), and Riley, Stommel, and Bumpus (1949), develop a model that determines the levels of phytoplankton and zooplankton population in the northwest Atlantic. The situation is similar to the situation at Wood River. Data that Riley fitted his model to are similar to those from Wood River.

We hope that the Riley model can be fitted to the data from the Wood River system.

Riley (1946) expresses the rate of change of phytoplankton as:

$$\frac{\partial P}{\partial t} = P (P_h - R_p - G),$$

where

P = phytoplankton population,

P_h = photosynthetic rate,

R_p = respiratory rate, and

G = grazing rate.

Riley then derives equations for these various rates. Riley assumes first that chlorophyll concentration is proportional to plant biomass. Given that nutrients are not limiting, then photosynthesis is a function of light intensity:

$$P_h = pI,$$

where

p = constant and

I = incident solar radiation.

Now light intensity varies with depth, and light intensity at depth z is given by:

$$I_z = I_0 e^{-kz},$$

where

I_0 = incident solar radiation,

k = extinction coefficient, and

z = depth.

If we know the depth of the euphotic zone, we can arrive at an average photosynthetic rate:

$$\bar{P}_h = \frac{I_o \int_0^{z_1} p I_o e^{-kz} dz}{z_1} = \frac{p I_o (1 - e^{-kz_1})}{kz_1}$$

where

z_1 = depth of the euphotic zone.

Photosynthetic rates are modified by nutrient depletion and by turbulency, which carries the breeding stocks out of the euphotic zone. In Riley's earlier papers, modifications are expressed simply by multiplying the mean photosynthetic rate by $(1-N)$ and $(1-V)$, where N = rate of nutrient depletion and V = rate of turbulency.

These ideas extended in Riley's later papers. The nutrient-phytoplankton relations in the oceans are different from those in an oligotrophic lake such as the Wood River lakes. The presence of a thermocline, which is above the maximum depth of the euphotic zone, may negate the effects of turbulency as Riley defines it.

A fix on the effects of nutrient limitation can be achieved by comparing maximal phytoplankton biomass, which can be given from the model without any nutrient consideration, and by comparing those to observed phytoplankton biomass.

Respiratory rate is a function of temperature:

$$R_p = R_{p0} e^{r_p T}$$

where

R_{p0} = rate @ 0°C,

r_p = constant, and

T = temperature.

Riley assumes that herbivore grazing rate is proportional to herbivore density, because the zooplankton in his study area were filter feeders:

$$G = gZ,$$

where

G = grazing rate,

g = constant, and

Z = herbivore population.

Substitution of these rate equations into the original equation yields:

$$\frac{\partial P}{\partial t} = P \left[\frac{PI_0}{kz_1} (1 - e^{-kz_1})(1 - N) - R_{po} e^{r_p T} - gZ \right].$$

Riley (1947a) expresses the rate of change of the herbivore population as:

$$\frac{\partial Z}{\partial t} = Z(A - R_z - C - D),$$

where

Z = herbivore population,

A = rate of assimilation of food by the herbivore,

R_z = herbivore respiratory rate,

C = predator consumption rate, and

D = herbivore death rate.

The assimilation rate is proportional to the phytoplankton population, but there is a maximal rate of assimilation, which Riley claims is 87 percent of the animal's weight per day:

$$\begin{aligned} A &= xP, \quad xP < A_{\max} \\ &= A_{\max}, \quad xP \geq A_{\max}, \end{aligned}$$

where

x = constant,

A = assimilation rate,

A_{max} = maximum assimilation rate, and

p = phytoplankton population.

Respiration is assumed to be a function of temperature and not affected by any other factor, thus:

$$R_z = R_{z0} e^{r_z T},$$

where

R_z = respiratory rate,

R_{z0} = respiratory rate at 0°C,

r_z = constant, and

T = temperature.

The rate of consumption of herbivores by predators is proportional to the number of predators, thus:

$$C = cS,$$

where

C = rate of consumption by predators,

c = constant, and

S = predator population.

The natural mortality or death rate is assumed to be constant:

$$D = D.$$

Substituting into the original equation, we have:

$$\frac{\partial Z}{\partial t} = Z \left[xP - R_{zo} e^{r_z T} - cS - D \right].$$

So far, we have not mentioned how the zooplankton and phytoplankton relate to production of sockeye salmon. Brockson et al. (1970) present a trophic dynamic model, which was based on data from three sockeye salmon systems similar to the Wood River system. One purpose of our study was to further substantiate the Brockson model. We have found that, although some relations presented in the above paper hold in the Wood River system, others do not.

The Brockson model is based on a few simple density-dependent relations: first, that sockeye growth rate is inversely proportional to sockeye biomass; second, that sockeye growth rate is proportional to zooplankton biomass up to some maximal growth rate; and third, that zooplankton biomass is inversely proportional to sockeye biomass. The first relation implied that interspecific competition at high population densities lowers the growth rate. The third implies that the sockeye exert a cropping force on the zooplankton population. With these relations in mind, Brockson says that the production of sockeye can be determined wholly from growth rates and biomasses of lower trophic organisms on which the salmon feed.

In the Wood River system, the biomass of sockeye depends heavily upon parent egg deposit, which varies greatly from year to year, and is completely independent from the biomass of food organisms. Lake levels and winter conditions do affect the survival of the eggs. These are density-independent factors and may explain why the correlation of relations 1 and 3 above are -1.10 and -0.07, although sockeye correlation between growth and zooplankton density is +0.44.

The model presented by Brockson may not be adequate in explaining higher trophic level phenomena. But, in the lower trophic levels, where zooplankton and phytoplankton are distributed somewhat uniformly over the lake, a simple model like Riley's may work. The situation in the

higher trophic levels is more complex. Organisms are not distributed uniformly. They exhibit complex behavior. Migration patterns are more complex than passive sinking or drifting with lake water movements, as with plankton. Fish move around the lake. They are littoral fish in the spring and pelagic during the summer and winter. Therefore, behavioral considerations perhaps must be included in a strategy type of model, if one is to model effectively ecosystems containing complex organisms such as fish.

REFERENCES

- BROCKSEN, R. W., G. E. DAVIS, and C. E. WARREN. 1970. Analysis of trophic processes on the basis of density-dependent functions. IN: J. H. Steele [ed.], Marine food chains. p. 468-498. University of California Press.
- FLEETING, R. H. 1939. The control of diatom population by grazing. *J. Cons. Int. Explor. Mer.* 14(2):210-227.
- GILBERT, J. R. 1968. Surveys of sockeye salmon spawning populations in the Nushagak District, Bristol Bay, Alaska, 1946-1958. University of Washington, Publ. in Fish., New Ser. 3:199-267.
- RICHARDS, F. A., and T. G. THOMPSON. 1952. The estimation and characterization of plankton populations by pigment analysis. A spectrophotometric method for its estimation of plankton pigment. *J. Mar. Res.* 11:156-172.
- RILEY, G. A. 1946. Factors controlling phytoplankton population of Georges Bank. *J. Mar. Res.* 6(1):54-73.
- RILEY, G. A. 1947a. A theoretical analysis of the zooplankton population of Georges Bank. *J. Mar. Res.* 6(2):104-113.
- RILEY, G. A. 1947b. Seasonal fluctuations of the phytoplankton population in New England coastal waters. *J. Mar. Res.* 6(2):114-125.
- RILEY, G. A., and D. F. BUMPUS. 1946. Phytoplankton-zooplankton relationships on Georges Bank. *J. Mar. Res.* 6(1):33-47.
- RILEY, G. A., H. STOMMEL, and D. F. BUMPUS. 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bing. Oceanogr. Coll.* 12(3):1-169.
- ROGERS, D. E. 1967. Estimation of pelagic fish population in the Wood River lakes, Alaska, from tow net catches and echogram marks. Ph.D. thesis, University of Washington, Seattle. 91 p.
- ROGERS, D. E., D. H. SILER, and T. CROKER. 1970. A summary of climatological observations and water temperatures in the Wood River lake system. University of Washington, Fish. Res. Inst. Circ. 70-10. 38 p.
- RYTHER, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. *Limnol. and Oceanogr.* 1:61-70.
- STEELE, J. H. 1958. The quantitative ecology of marine phytoplankton, *Biol. Rev.* 34:129-158.

Table 1. Data available for Wood River lakes trophic relation model.

Measurement	Lake	Years	Number of dates per year	Number of stations per date
Chlorophyll "a" (mg/m ³) Secchi depth (m) Total alkalinity (mg/l CaCO ₃) pH	Aleknagik	1961-70	4	2
	Nerka	1961-62	4	4
	Little Togiak	1961-62	3	2
	Beverley	1961-62	2	2
	Kulik	1961-62	2	2
Primary production (mg C/m ² /4 hr)	Aleknagik	1962-70	4	2
	Nerka	1962	4	4
	Little Togiak	1962	3	2
	Beverley	1962	2	2
	Kulik	1962	2	2
Zooplankton (number/m ³)	Aleknagik	1961-70	4	6
	Nerka	1961-62,	1	18
		1967-70	1	
	Little Togiak	1961-62,	1	3
		1967-70	1	
	Beverley	1961-62,	1	6
		1967-70	1	
	Kulik	1961-62,	1	6
1967-70		1		
Fish abundance and size June-July (number/beach seine haul and mean length)	Aleknagik	1962-70	6	10
	Nerka	1969-70	1	5
	Beverley	1968-70	1	9
	Kulik	1968-70	2	9
Fish abundance and size, August-September (population estimate, mean length, and biomass; one estimate per year per lake)	Aleknagik	1958-70	2	24
	Nerka	1958-70	1	72
	Little Togiak	1958-70	1	10
	Beverley	1958-70	1	30
	Kulik	1958-70	1	24
Survival of sockeye fry from potential eggs (%)	Aleknagik	1958-70	1	
	Nerka	1958-70	1	
	Little Togiak	1958-70	1	
	Beverley	1958-70	1	
	Kulik	1958-70	1	

Table 1. Data available for Wood River lakes trophic relation model -
Continued

Measurement	Lake	Years	Number of dates per year	Number of stations per date
Growth rates of sockeye fry and threespine sticklebacks during the summer (mm/day) 5/31 9/15	Aleknagik	1959-70	1	
	Nerka	1958-70	1	
	Little Togiak	1958-70	1	
	Beverley	1958-70	1	
	Kulik	1958-70	1	
Abundance of adult sockeye (number of spawners) by age and sex	Aleknagik	1946-70	1	
	Nerka	1946-70	1	
	Little Togiak	1946-70	1	
	Beverley	1946-70	1	
	Kulik	1946-70	1	
Water temperature (surface, 0-20m, and 0-bottom, °C)	Aleknagik	1958-70	4-10	6-10
	Nerka	1958-70	1	13
	Little Togiak	1958-70	1	3
	Beverley	1958-70	1	6
	Kulik	1958-70	1	6
Solar radiation (gm/cal/cm ² /day)	Aleknagik	1961-70	daily (June-Sept)	1
Lake level (cm from bench mark)	Nerka	1952-70	daily (June-Sept)	1
Air temperature (°C) and precipitation (in)	Dillingham (for Wood River lakes)	1919-70	monthly (Jan-Dec)	1
Calculated weight at 5/31 for age 0 sockeye and age I sticklebacks	Aleknagik	1959-70		
	Nerka	1959-70		
	Little Togiak	1959-70		
	Beverley	1959-70		
	Kulik	1959-70		

Table 2. Variable values from Lake Aleknagik, 1958-1970

Year	fry population (millions)	parent egg deposit (millions)	biomass fry, age 0 (10 ⁶ grams)	biomass fing., age 1 (10 ⁶ grams)	biomass sticklebacks (10 ⁶ grams)	instantaneous per day growth rate 5/31 — 9/1	Sept. 1 mean weight red fry (grams)	May 31 mean weight red fry (back calculated) (grams)	instantaneous per day growth rate, age I sticklebacks 5/31 — 9/1	Sept. 1 mean weight age I sticklebacks (grams)	May 31 mean weight age I sticklebacks (back calculated) (grams)	% survival sockeye eggs — fry	peak level at spawning (cm)	mean air temp. Dec.-Jan. (-°C)	mean water temp. 0-20 m at spawning, (°C)	dev. from mean date of ice breakup	lake level July (cm from ref.)	lake level August (cm from ref.)	water temperature 0-20 m (°C)	water temperature heat budgets	solar radiation July (gram cal./cm ² /day)	solar radiation August (gram cal./cm ² /day)	zooplankton 7/19-8/15 (# per m ³ x 1000)	zooplankton 8/16-9/10 (# per m ³ x 1000)	chlorophyll "a" July	chlorophyll "a" August	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26		
1958	6.3	198	13.6	1.7	10.3		2.15			0.66		3.2	32	13.2		-18	176	107	11.3	20.8							
1959	4.6	130	10.3	0.8	68.7	0.32	2.22	0.13	.019	0.76	0.18	3.6	107	9.2	11.3	-4	88	60	11.8	18.6							
1960	29.5	445	45.4	0.3	13.3	0.24	1.54	0.14	.12	0.61	0.27	6.6	60	11.6	11.8	+2	105	103	11.4	18.5							
1961	24.7	212	44.1	20.4	10.6	0.26	1.79	0.17	.15	0.56	0.18	11.6	103	4.7	11.4	-3	87	81	11.3	16.3	323	257	5.1	4.9	1.96	1.41	
1962	12.4	394	17.7	3.2	29.0	0.21	1.43	0.21	.15	0.62	0.21	3.1	81	12.6	11.3	0	116	62	12.1	19.8	408	271	2.7	3.2	1.36	0.84	
1963	6.8	109	14.6	1.0	26.3	0.18	2.15	0.45	.17	0.75	0.19	6.2	62	7.1	12.1	1	104	72	11.9	18.0	397	316	7.4	6.1	1.31	0.94	
1964	6.6	69	13.0	1.5	77.1	0.32	1.98	0.10	.15	0.60	0.20	9.6	72	7.8	11.9	14	116	68	10.6	17.8	428	281	4.0	7.3	2.06	1.74	
1965	20.3	356	28.2	0.3	39.7	0.27	1.39	0.11	.15	0.46	0.15	5.7	68	13.6	10.6	4	122	74	11.1	18.7	402	300	4.6	1.8	1.99	1.24	
1966	43.5	551	42.2	34.2	30.8	0.21	0.97	0.13	.18	0.46	0.12	7.9	74	10.5	11.1	5	138	90	10.1	17.4	386	266	3.9	6.0	1.17	0.61	
1967	13.3	690	9.8	5.5	12.0	0.18	0.74	0.19	.17	0.53	0.16	1.9	90	10.3	10.1	-3	93	59	12.2	15.7	444	276	2.2	2.6	0.69	0.40	
1968	2.4	210	4.2	0.4	28.7	0.27	1.75	0.19	.15	0.61	0.23	1.1	59	8.9	12.2	-1	67	66	12.6	15.8	394	328	6.5	8.0	1.54	0.92	
1969	19.2	380	40.0	0.1	35.0	0.26	2.08	0.18	.15	0.62	0.22	5.1	66	12.0	12.6	1	129	58	10.6	14.5	308	329	5.5	7.1	1.72	0.69	
1970	10.6	328	19.6	0.4	30.4	0.32	1.85	0.13	.15	0.62	0.23	3.2	58	-9	10.6	-9	122	92	10.8	17.1	345	282	6.0	7.2	1.34	1.00	

Table 3. Patterns of Phytoplankton and Zooplankton Changes through the Summer in 1961-1970, along with Carbon Production and Solar Radiation.

Date	Zooplankton per m ³	Carbon in 4 hr	Chlorophyll "a"	Solar radiation
		Mg/m ²	Mg/m ³	G cal/m ² /day
June 20-26	2,855	67.0	122.0	462.3
July 11-20	3,322	55.0	152.0	383.5
August 5-13	4,827	56.4	97.9	290.6
September 5-11	5,348	66.8	95.7	217.2