

## Analytical Non-linear Modular Dynamics for Balanced Exploitation of Fisheries

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### Abstract

Analytical Modular Dynamics (AMD), is a non-linear theory based on differential geometric analysis of 2nd order Ode's(SODE's) and is used here to formulate two fishery models subjected to Balanced Exploitation (BE). Both population (linear) stability, and production (Jacobi) stability, are investigated using Volterra-Hamilton Systems. The first model is of 2-species in stable competition, but experiencing BE. The maximum sustainable yield is obtained for a harvesting efficiency which is linear in the population densities. The second is of individuals in a shoal having large numbers of fish subjected to BE. The mathematical theory implies interesting social interactions, such as shoal breakdown into separate schools. Some open problems are stated.

### Key Word and Phrases

Balanced Exploitation, Fisheries, Harvesting Yield, Second Order Ode's, Differential Geometry, Weak Chaos, Formal Modular Populations, Volterra-Hamilton Systems, Medawar Growth Energy, Energy Budgets

### Introduction to the AMD Method

Almost every individual plant or animal is a large cell population, in fact, a large set of cell populations, all distinct. The cell populations composing an individual or a colony communicate chemically with each other and with the ambient environment which may include other plants, animals as well as non-biotic factors. The plant-plant interactions are mediated by allelochemicals (phenolics, terpenes, lignins, etc.), while plants-herbivore interactions involve a list of allomones and kairomones, (eg., [35], [31]). Our project to quantify and describe chemically based ecology, using second order ordinary differential equation models (SODE's), started in, 1980, and was based on recognizing that the fundamental variables were two:  $X$ , the produced biomass from *all members*, and  $N$ , the set of the of *all producers*, [24],[1],[2]. Such an idea does not occur in the 20th century until the plant ecology work of, John L. Harper, [24]. A dynamical approach to chemical interactions was developed using Volterra-Hamilton systems, which are special special SODE's, and Harper's criteria, [2], [3].

Our AMD research program was eventually augmented with the geometrical perspective of KCC-Theory, [27], [19], [20], and Finsler Geometry, [8], [6], [5]. Analytical Modular Dynamics, (AMD), is focussed on the deeper geometric properties of SODE's, those invariant under coordinate changes, and singles out curvature measures for a major role in production dynamics. It is curvature invariants which determine completely the stability of the paths of production. Curvatures are defined in terms the interaction pattern (connection) of the set of producer populations. Interestingly, the applications using Finsler geometry arose because of density-dependent (social) interactions in ecology, [8], [6]. These "higher order" interactions were discovered in early field studies, [26], and experiments performed in the '70's by, G.E. Hutchinson, and his students at Yale University, [23], [37], [38]. While computations in the SODE-KCC-Finsler models had been long and difficult, over the last 15 years, calculation accuracy has been improved and time required shortened, by S.F. Rutz's package, FINSLER, [5],[32]. This was published in 2003 as a CD included with the second of the two volumes of [5]. A recent paper, [39], has made corrections to the original FINSLER and we here publically thank the authors. We had not been able to circumvent Springer's copyright laws to make corrections, ourselves.

In the present work, which uses FINSLER, we concentrate on SODE's which are actually quadratic and naturally include  $n$ -dimensional Riemannian geodesics. Interaction (connection) coefficients are allowed to depend on *slowly varying*  $X$  so are (approximately) constant over short enough time intervals. The associated stochastic theories we developed for the project are not discussed here. They have been published elsewhere (see reference list).

In order to treat colonial organisms, our group used Harper's idea that an individual organism is a set of modular units of production, [24]. Here, in Part 3, it is extended to cover individual vertebrates. An individual is taken to be the single population of all its cells, which are the modular units used in the mathematical theory. Moreover, it is natural to use allometric growth concepts in AMD. Allometries were first investigated experimentally for animals in the 1930's by Sir Julian Huxley and Sir Joseph Needham, and by, A. Laird, [28], for vertebrates in the 1960's, and by S.J. Gould, [22], in the 1970's, for paleontology. Recently, more mathematical works have been published [6].

Our method is called *Analytical Modular Dynamics* (AMD) and within it, each organism is considered to be not only a collection of its organs, but also a set of populations of cells comprising those organs, at least formally. For example, an individual plant or animal has its organs grow in Gompertz fashion and do so at the same rate,  $r$ , according to the experiments of, A. Laird, [28], and J. Harper, [24]. Furthermore, starting with a single vertebrate embryo, ontogeny progresses and ultimately culminates in the adult form at sexual maturity.

Depending on the modelling problem at hand, some organs will play a small role, or even no role at all, in any modelling effort. For instance, in fisheries modelling, the ovaries and testes of an individual would seem relevant, while the gills and brains may not. Furthermore, the chosen organs, their cell constituents, and chemical compounds they produce, will be relevant to a particular problem and these will form the populations of *modular units* for the AMD method. Invariably, there will be several possibilities for defining modular structures. For example, it would be possible to approach fishery reproduction models using, say, the liver (for females) and kidneys (for males), [33]. But, although liver and kidney formulations might be fine for a physiological problem, it is probably more detail than is needed for fisheries study. Naturally, the ovaries and testes could, as well, be used as the organs of choice. Yet, for the fishery problems it is conceptually simpler to view the whole individual, as the organ of choice, while stipulating that eggs or sperm are the relevant compounds produced. So, for any particular individual, its entire cell population,  $N$ , produces the log-biomass of sperm or eggs,  $X$ , and these two variables are to be viewed as continuous (smooth) in some time interval of study. Finally, to make this presentation more concrete, the 3-spined stickleback, *Gasterosteus aculeatus* L., referred to in the text, has a well understood reproductive cycle in the wild, [33].

### 1. Balanced Exploitation of a Two-Species Competition

For modelling biomes with Analytical Modular Dynamics (AMD), it is required to select two types of independent phase-space variables,  $X$  and  $N$ . These are, respectively, net biomass,  $X$ , produced by a population (species or class)  $\Sigma$ , and the large number  $N$ , of its producers, [1], [8], [6], [10], [17], [21], [24], [35]. There are also, surrogate variables, which by definition are allometrically related to total production,  $X$ . Measuring  $X$  includes discounting repair and maintenance of existing biomass of  $\Sigma$ , because this is what *net production* means. To be specific, consider a school of 3-spined Sticklebacks, during a reproductive cycle. All fish are about the same size, and *total* egg biomass,  $m_e$ , is allometrically related to *total* ovary biomass,  $m_o$ . Consequently, larger  $m_o$  will result in larger  $m_e$ . In other words, the Huxley/Needham Allometric Law,

$$X_e = \ln(m_e) = a \cdot \ln(m_o) + b = a \cdot X_o + b, \quad (1.1)$$

holds for some constants  $a > 0$  and  $b$ . A similar relationship holds for sperm biomass,  $m_s$ , produced and the testes biomass,  $m_t$ , producing it. The allometric relationship (1.1) is typical for surrogates of biomass in AMD theory. It follows that  $m_e$  and  $m_s$  are allometrically related, that is,  $X_e$  and  $X_s$  are linearly related. This will be important below.

There are interpretations other than the reproductive one. For feeding fish shoals, it is known that chemically induced olfactory cues in diet-mediated shoals having several species, form a basis

for nearest-neighbor associations and thereby promote shoal cohesion. The feeding fish produce a chemical substance diffused through surrounding water, thereby inducing a behavioral response in hungry fish. Namely, the hungry fish move into nearest-neighbor arrangements with those feeding or replete fish. The *total* amount of chemical released is reasonably assumed allometrically related to *total* intake of nutritional biomass. A larger *i*th total nutritional intake,  $X^i$ , implies a larger *i*th total amount of chemical released into the water column which, in turn, cues an olfactory response in fish nearby. Within the (AMD) approach each chemical is identified by the subset of fish producing it. It may be identical to cues produced by fish of a different subset within the shoal.

Consider, now, a model for Balanced Exploitation, where the two ( $n = 2$ ) populations involved compete for common food resources and there is a positive stable equilibrium,  $(N_1^*, N_2^*)$ . For models of shoals and schools, it is assumed the two intrinsic growth rates ( $\lambda$ ) are equal. This is reasonable for schooling fish which are usually all about the same size. The constant coefficient Volterra-Hamilton System (VHS) is the SODE ( $k_1 = k_2 = 1$ , unless stated otherwise; see remark after Theorem A):

$$\begin{aligned} \frac{dX^1}{dt} &= k_1 N^1, & \frac{dX^2}{dt} &= k_2 N^2, \\ \frac{dN^1}{dt} &= \lambda N^1 - \gamma_1 (N^1)^2 - \gamma_2 N^1 N^2 - \varepsilon(X, N, t) N^1, \\ \frac{dN^2}{dt} &= \lambda N^2 - \delta_1 (N^2)^2 - \delta_2 N^1 N^2 - \varepsilon(X, N, t) N^2. \end{aligned} \tag{1.2}$$

The first two equations are the fundamental Volterra Production Equations, [34] (see [2] for an professional English translation from the original French), which say population,  $N$ , produces a biological material or chemical compound,  $X$ , monotonically increasing in time. There are certain conditions on the *positive constant* coefficients which ensure this classical competitive interaction has a steady-state, namely,

$$\gamma_1 > \delta_2 \quad \text{and} \quad \delta_1 > \gamma_2. \tag{1.3}$$

These equilibrium conditions are augmented with certain conditions on  $\varepsilon$ . Note that is the same for each equation (a sort of *unbiased mortality rate*) and for the  $n = 1$  case, assumed constant. This is often the case, but here it is taken to be linear in  $N$ . Yet, it could as well be taken (positively) first-degree homogeneous in  $N$ , which is more general (i.e., scales linearly, but is not linear), [1], [7], [8], [9], [16], [11].

The linearity (or homogeneity) is closely related to the concept of *heterochronic* change, previously used to describe: (1) plastic deformations of phenotype (work in progress); (2) time-sequencing changes during ontogeny, [8], [12], [30]; (3) succession in plant communities, [21], [16], [35]; and (4) biological evolution, [36], [6], [8], [14], [25]. Heterochronic change is a concept defined using classical projective differential geometry, [5], [8], [6]. It is understood as a change in production parameter,  $S \rightarrow P$ , simultaneously accommodating a change in the coefficients of interaction and by definition must always be induced by an external source.

Also,  $\partial_t \varepsilon = 0$ , so that (BE) Balanced Exploitation  $\varepsilon$  is *not explicitly time dependant*. Nevertheless,  $\varepsilon$  may depend on  $X$  and obviously depends on  $N$ , both of which vary in time. One instance of this occurs when a shoal is monitored during feeding to determine if it is well-fed ( $X$  large nutritional intake) or not ( $X$  small). The magnitude  $\varepsilon$  should be carefully monitored with the  $X$ - output readings, at least if preservation of the social community (e.g., shoal) is desired. A similar remark holds when a social community is engaged in mating rituals. For the precise expression, write:

$$\varepsilon = e_1 N^1 + e_2 N^2, \quad (1.4)$$

where the  $e$ 's are positive constants. There are natural constraints on  $e_1, e_2$ , if stability is to be preserved.

We now give a proof for existence of maximal sustainability for a certain constraint condition:  $e_2 = k e_1, k > 0$ . We may further suppose that each coefficient of the quadratic terms of (1.2) is a multiple of  $\lambda$ , for then all the lambdas cancel when  $dN^1/dt = dN^2/dt = 0$ , to compute the steady state. We use the simpler notation  $e_1 = u$  and write the yield vector's two components and the steady-state as:

$$Y^i = (uN^1 + kuN^2)N^i,$$

$$N_*^1 = \frac{\delta_1 - \gamma_2}{\gamma_1(\delta_1 + ku) - \gamma_2(u + \delta_2) + u(\delta_1 - k\delta_2)}, \quad \frac{N_*^2}{N_*^1} = \frac{A}{C}.$$

from this, with  $Q = (A + kC)u + B$  and  $B = \delta_1\gamma_1 - \delta_2\gamma_2, C = \gamma_1 - \delta_2, A = \delta_1 - \gamma_2$ , we have steady-state yield vector components:

$$Y_*^1 = \frac{A(A + kC)u}{Q^2} \quad \text{and} \quad Y_*^2 = \frac{C}{A} \cdot Y_*^1.$$

Now, computing the first and second derivatives, with respect to  $u$ , of the steady-state yields and setting them to zero gives  $u_* = B/(A + kC)$ , the optimal harvesting efficiency, and at this value,

$$(Y_*^1)'' = -\frac{A + kC}{8B^3},$$

showing the yield at the steady-state is a maximum.

**Theorem A.** *Invariance of stability of the positive equilibrium of (1.2) under balanced exploitation,  $\varepsilon$ , holds whenever:*

$$e_1 < \gamma_1 - \delta_2 \quad \text{and} \quad e_2 < \delta_1 - \gamma_2.$$

The steady-state is given as:

$$\begin{aligned} N_*^1 &= \frac{\lambda \alpha_2}{\lambda \alpha_1 \alpha_2 + e_1 \alpha_2 + e_2 \alpha_1}, \\ N_*^2 &= \frac{\alpha_1}{\alpha_2} N_*^1 = \frac{K_2}{K_1} N_*^1, \end{aligned} \tag{1.5}$$

$$\lambda \alpha_1 = \gamma_1 - e_1, \quad \lambda \alpha_2 = \delta_1 - e_2, \quad \alpha_i K_i = \lambda, \quad i \in \{1, 2\},$$

where  $K_i$  is the  $i$ th population carrying capacity. Furthermore, the positive steady-state ratio is independent of  $\varepsilon$ .

Note that BE reduces the equilibrium population value, but not its ratio.

**Remark.** Production (or consumption) rates, per  $i$ th production unit, per unit time,  $t$ , are expressed

$$k_i = \frac{1}{N^i} \frac{dX^i}{dt} = 1$$

and for convenience, are taken to be unity in this paper. Usually,  $X$  is a log biomass (or a surrogate), denoted  $\ln(m)$ , so  $dX/dt = (1/m) \cdot dm/dt$ , generally. Some models employ variable  $k$ 's, but for the present they are fixed. Likewise,  $X$  can enter the coefficients of (1.2), but for the present, they are assumed *approximately constant*, or at least varying slowly in time. Finally, several models have used density-dependent interaction coefficients, but this entail a considerable amount of Finsler geometric technical apparatus and we will not pursue this here (see references).

The condition on  $\varepsilon$  necessary to ensure that the (linearly) stable state of the two (positive) population densities is preserved during balanced exploitation of the social community is just (1.5) above. But, what can be said about (Jacobi) stability of whole trajectories? If a portion of a social community starts out with stable production (or consumption), what happens when balanced

exploitation is applied? This is an important question. Why? For one thing, *reproduction* is a special kind of *production* and survival depends on reproductive stability. Fortunately, mathematical techniques of KCC-theory allow us to decide if production stability would be maintained during balanced harvesting. Related to reproductive stability are questions about costs, and conservation energy resources. For each of the two models we discuss, there is a *Medawar Growth Energy (MGE)*, which appears when total production,  $S$ , rather than clock time,  $t$ , is used as a growth parameter along production curves, [6]. Thus, substituting  $dS = e^{rt} \cdot dt$  in (1.2) removes the linear term and the SODE is in standard form and the form remains the same when a non-singular coordinate transformation is performed. For example, if we switch from one surrogate of allometric growth to any other (they are linearly related), the standard form does not change. It is certainly obvious what happens to  $dy^i/dS$  under such a linear change, but there is also the transformation of the coefficient array (called the *Connection*) to consider. It is well-known that all the differential geometric properties are invariant under non-singular coordinate transformations. In particular, the curvatures do not change. In differential geometry, this is known as the Law of Transformation of the Connection, [2], [8], [6].

A consequence of this invariance is that there can be no distinction between a male and a female fish in the models developed with AMD. This is because the logarithm of egg and sperm biomass are linearly related, that is, they are allometrically related surrogates of total fish biomass.

The MGE functional does not change value along these curves. However, MGE attains new values under balanced exploitation, and these values, in turn, are conserved throughout the growth process. We mention this again in Part 3. We end this section with the expression of the (log of) MGE, for (1.2):

$$\ln[MGE] = Q(X) + \left(1 + \frac{1}{\lambda}\right) \ln(F^2) - \frac{1}{\lambda} \ln(F^1),$$

$$Q(X) = -(\alpha_1 + e_1)X^1 + [(1 + \lambda)\alpha_2 + e_2]X^2 + \nu X^1 X^2. \quad (1.6)$$

MGE is constant along any solution of (1.2) as is readily checked by taking the total derivative with respect to  $S$  along that solution. Before BE, we have  $e_1 = e_2 = 0$ , while after BE, we do not.

## 2. Shoals of Individual Fish: Their Breakdown into Schools

Consider a *single* fish moving with the school, say, an individual 3-Spined Stickleback. Following the multi-species experimental work of A. Laird, [28], we know the pattern of total biomass growth,  $m_r$ , from fertilized egg to adult, is best described by the famous *S-shaped* Gompertz curve with *rate parameter*,  $r = \lambda$ . In fact, Laird discovered that among vertebrates, an internal organ's growth,  $y = \ln(m_o)$ , in a single individual is described by a Gompertz curve.

Moreover, these organs all have the same *rate parameter for that individual*. This experimental result, as Laird observed, actually explains the Huxley/Needham-Allometric Law, for vertebrate organs, [ibid].

Now consider modular units to be the cells of an individual Stickleback, [33]. The log biomasses,  $y_o$ ,  $y_t$  are taken to be egg clutch biomass and sperm biomass, respectively, and are solutions of the (SODE) initial-value problem (Laird's Law):

$$\frac{d^2y}{dt^2} + \lambda \frac{dy}{dt} = 0, \quad y(0) > 0, \quad \frac{dy}{dt}(0) > 0. \quad (2.1)$$

(2.1-A)
(2.1-B)

Clearly, if  $Z(t)$  is a solution of (2.1-A), then any linearly related variable with the specified initial conditions is also a solution. Therefore, within AMD there is no distinction between a given surrogate variable and any other, for they are allometrically related. The particular solution is:

$$\ln(m(t)) = y = \ln(a) - ce^{-rt},$$

where  $a$ ,  $c$  and rate,  $r = \lambda$ , are all positive constants. The  $y(t)$  graph is concave down and asymptotically approaches,  $\ln(a)$ . It follows easily that  $m(t)$  is indeed a Gompertz curve, [6].

We need to connect the population-centered, Part 1, to the individual- centered, Part 2. Let's start from the standard 1- species classical *harvesting efficiency equation* for population,  $N$ . That is,

$$\frac{dN}{dt} = rN - \frac{r}{K}N^2 - \epsilon N,$$

where  $r$ ,  $K$ , and  $\epsilon$  are positive constants, the last being the classical harvesting efficiency. However, in the present work, interest is in balanced exploitation and our considerations turn to  $\epsilon = e \cdot N$ . This is due to our interest in exploitation of a (size  $N$ ) school of fish and its whole-population effects. Unbiased exploitation as a harvesting strategy falls into this category. Let's look in detail at balanced harvesting in this 1-dimensional case. The steady-state is  $N_* = rK/(r + eK)$ , the yield is  $Y(e) = er^2K^2/(r + eK)^2$ . The graph of  $Y(e)$  starts at the origin and increases to a stable maximum at  $e = r/K$ . There is a point of inflection at  $e = 4r/K$ , after which  $Y$  tends to zero, asymptotically, as  $e$  becomes unboundedly large.

The cells of male or female Sticklebacks are the populations of modular units,  $N$ , assumed to grow according to a logistic pattern. These modules produce  $X$ , the eggs and sperm. But, as Laird demonstrated, total biomasses better fit Gompertz curves than logistic ones (both are S-shaped),

[28]. Likewise, the Noble Laureate in physiology, Sir Peter Medawar, did extensive experiments on cultured heart cells of chicken embryos and found the cell population growth biomass better fit a Gompertz curve than a logistic, [29]. He introduced, in the same work, the concept of *growth energy* (MGE) for cell populations in culture which we mentioned in Part 1.

As is well-known, population models for ecology and evolution are founded on the logistic differential equation ( $r$ - and  $K$ -selection, etc.), as in (2.2) with  $\varepsilon = 0$ , rather than on the Gompertz one, from (2.1), [22]. The “population growth versus individual growth” dilemma is mathematically resolved in [6], where it is referred to as “Harper’s Criterion” (which considers a plant as both an individual and a population), [24]. In fact, this dilemma is not new. In the 19th century, the British biologist known as “Darwin’s Bulldog”, T.H. Huxley, the grandfather of Sir Julian Huxley, argued with the great naturalist, L. Agassiz, over the status of the Portuguese Man-of-War, a member of order Siphonophora. Huxley thought it was an individual, while Agassiz, founder of the National Academy of Science in the USA, thought it a population. Today’s scientists know it is both. It may be useful to give a mathematical description of this duality. We use the Stickleback as concrete example, but many vertebrates would make good examples, as well.

A Stickleback’s biomass,  $m(t)$ , follows a Gompertz curve, or equivalently taking logarithms,

$$\ln[m](t) = \ln a - ce^{-rt}.$$

Sexual maturity happens at value  $m(\infty) = a$ , or equivalently,  $\ln[m(\infty)] = \ln a$ . The Formal Modular Population (FMP),  $N(t)$ , associated to the Gompertz, is a Logistic population, and is given by:

$$N(t) = \frac{K}{1 + rce^{-rt}} \quad (2.2)$$

This FMP is specified by the two parameters  $r$  and  $K$ , via:

$$K = [1 + r(\ln a - \ln[m(0)])]N(0).$$

For vertebrates, one can always take  $N(0) = 1$ , since growth starts with a single fertilized egg. Note that if  $r$  and the initial biomass,  $m(0)$ , are known, then, from (2.3),  $K$  is defined uniquely by  $\ln a$ , which it approaches asymptotically.

In summary, growth of an individual has a uniquely associated FMP which grows logistically, while that individual’s biomass accumulates via Gompertz.

Making use of a variable originally introduced by J. Huxley, namely, the *relative proportions variable*,



$$x^* = \frac{K - N}{N},$$

note that the pair of equations:

$$\frac{dx^*}{dt} = -rx^* \quad \text{and} \quad \frac{dy}{dt} = x^* \quad (2.3)$$

where  $y(t) = \ln(m(t))$ , is equivalent to Laird's Law (2.1) and is also equivalent to the pair of equations:

$$\frac{dy}{dt} = \frac{K - N}{N} \quad \text{and} \quad \frac{dN}{dt} = rN \frac{1 - N}{K}. \quad (2.4)$$

with initial conditions  $y(0) = \ln a - c$  and  $N(0) = K/(1 + rc)$ , as in (2.1-B).

Use has been made of both individual growth (Gompertz/Laird pattern) as in (2.1) and population growth (Logistic pattern) as in (2.4). It is clear that  $N$  is precisely defined in terms of  $K$  and  $dy/dt$ . Once a  $K$  value has been specified, the Gompertz description gives precisely the logistic description according to (2.3) and (2.4). Thus, the individual-based view and the population based view are dual in a sense.

**Remark.** There is a mathematical fact about duality worth mentioning. It was first pointed out by S.F. Rutz and her student, Lucianna H.S. dos Santos in, 2010. It is stated as:

**Proposition B.** *Ratio  $m(t)/N(t) \searrow 0$  asymptotically if  $\lambda c \leq \lambda - 1$ ; if not, the ratio increases for a short time and then decreases to zero, asymptotically.*

Now, we introduce the concept of Net Growth,  $y(t)$ , which necessarily includes repair and maintenance,  $R_0$ , of growing tissues. Note that the notation  $y(t)$  is the same as used above for  $\ln(m(t))$ . The reason will be apparent. Define Net Growth for (2.4) as:

$$k \cdot y(t) = k \cdot y(0) + \int_0^t [k \cdot N(s) - R_0] ds. \quad (2.5)$$

Note that as  $N \nearrow K$ , the net growth  $y(t) \searrow 0$ , while repair and maintenance,  $R_0$ , approaches the constant value,  $kK$ , necessary to repair and maintain the entire adult, [35], [6]. As previously stated, we take  $k = 1$  for simplicity and  $y(0) > 0$ ,  $\frac{dy}{dt}(0) < 0$ , for initial conditions. Using the derivative operator  $d/dt$  on  $y(t)$ , and the logistic equation (2.4), we arrive at:

$$\frac{d^2y}{dt^2} + \left(\frac{r}{K}\right) \left(\frac{dy}{dt}\right)^2 + r \left(\frac{dy}{dt}\right) = 0.$$

The Net Growth Equation, (2.6), below, is significant. It is the generalization of Gompertz growth for an individual which holds for modular unit populations. Note, in particular, that the condition of infinite carrying capacity,  $K = +\infty$ , implies (2.1). With this brief discussion completed, let's move on to modelling a fishery under balanced exploitation, BE. For several fish we would have, for  $i \in \{1, 2, \dots, n\}$ ,

$$\frac{d^2 y^i}{dt^2} + \frac{r}{K_{(i)}} \cdot \left( \frac{dy^i}{dt} \right)^2 + r \frac{dy^i}{dt} = 0, \quad (2.6)$$

where the parents around the index  $i$  indicates that no summation on repeated indices is implied (if no parents occurs, then summation from  $1$  to  $n$  is implied).

### 3. Shoals, Schools and Energy Budgets

Shoaling fish, during reproductive phases of their life cycle, (or during a feeding event) require an equation, like (2.1) above, *for each individual*. The linearity of (2.1) indicates that any surrogate of total biomass satisfies this equation. In other words, the differential equations of (AMD)-theory, (2.1), makes no distinction between total produced biomass measurements and their surrogates. Therefore, there is no distinction between ovary biomass or testes biomass produced.

It is convenient to index the individuals in a school with upper index  $i$ ; thus,  $y^i$  denotes the log-biomass of egg or sperm produced by the  $i$ th individual. Since there can be millions of individuals in a shoal, the indexing set can be *very* large.

A spawning event involves visual input and olfactory cues from schoolmates, [33]. In order to use Lotka-Volterra type equations, we need to add terms to (2.1) which account for reproductive behavior. Thus,

$$\frac{d^2 y^i}{dt^2} + G_{jk}^i \left( \frac{dy^j}{dt} \right) \left( \frac{dy^k}{dt} \right) + \lambda \frac{dy^i}{dt} = 0, \quad (3.1)$$

where the  $i, j, k$  run from  $1$  to  $n$ ,  $n$  being the large number of fish in the shoal. Repeated indices are

summed from  $1$  to  $n$ . Other than the linear growth term, each of the  $n$  equations has  $n^2$  quadratic terms (there are  $n^3$  of the 3-index  $G$ 's) and the coefficients are approximately constants, in keeping with classical modelling ideas. The  $G$ 's describe *sexual interactions* during the reproductive period

(for example, 4 months in Northern Summers, [33]). For the case (2.6), the  $G$ 's are given by:

$$G_{ii}^i = \frac{r}{K_i} \quad \text{and} \quad G_{jk}^i = G_{kj}^i = 0, \quad \text{if } i = j = k \text{ is false.}$$

Consider the Volterra Production Equations, one for each individual in the school,

$$\frac{dy^i}{dt} = k_{(i)}F^i, \quad i \in \{1, 2, \dots, n\}.$$

Here, the right-hand side is interpreted as *weight* (or *scaled size*) of the  $i$ th individual *and* no distinction is to be made between males and females in the model. We have assigned to the Formal Modular Population (FMP) of a given individual, a number, which is its weight in grams, characterizing this FMP. Any characterization must be determined completely by  $r$ ,  $K$ , and  $N(\mathbf{0})$ . Since we are dealing with a vertebrate organism rather than a palm tree, *weight* would be a natural choice, just as in classical animal ecology. So  $K$  is understood as weight in grams at sexual maturity.

The relationship (3.2) implies that during spawning, the  $i$ th (logarithm of) sperm biomass,  $\ln(m_s^i)$ , and the  $i$ th (logarithm of) egg biomass,  $\ln(m_e^i)$ , are increasing over a time interval. We have taken the  $n$  positive proportionality constants,  $k_i$  equal to unity, for simplicity. The system (3.1) now reads:

$$\frac{dy^i}{dt} = F^i \tag{3.2}$$

$$\frac{dF^i}{dt} = -G_{jk}^i F^i F^k - \lambda F^i.$$

Since each fish is physiologically optimal in design by genomic programming and phenotypic response to environmental cues, and because social cohesion in a spawning school optimizes many of life's factors, (like protection from predation by nearest neighbor packing within the shoal, or food resource location via olfactory and visual cues), it would seem to further improve school-life to require optimization of total production of all  $y^i$ , simultaneously. But how is optimality judged?

What cost criteria or energy usage should be used to make this judgement?

An answer is (MGE), the Medawar's Growth Energy, [29], [6], which, expressed most simply as a quadratic form, is given by

$$MGE = g_{ij}(\mathbf{y})F^iF^j, \tag{3.3}$$

where the  $g$ 's are determined using the calculus of variations, [6], constrained by the constant coefficients condition in (3.2). The answer (unique, given the hypotheses stated) is called the Fundamental Theorem of Volterra-Hamilton Systems, [8], [6], is (up to a multiplicative positive constant)

$$g_{ij}(\mathbf{y}) = e^{\alpha_k y^k} \delta_{ij}, \tag{3.4}$$

where the  $\alpha_k$  are  $n$  constants (taken positive) and the  $G$ 's are given ( $i \neq j \neq k$ ) by:

$$\begin{aligned}
 G_{ii}^i &= \alpha_i, & G_{ij}^i &= G_{ji}^i = \alpha_j, \\
 G_{jj}^i &= -\alpha_i, & G_{jk}^i &= 0.
 \end{aligned}
 \tag{3.5}$$

The *assumption*, here, is: Each individual in a school interacts with at least one other in the school.

**Theorem** (Shoal Structure Theorem). *The model shoal breaks down into a set of schools, each described by (3.4) and (3.5). Each school is isolated from all others.*

**Remark.** The case of  $n$  independent individuals, (3.1) is the no-interactions case and would be covered in Theorem B accept the hypothesis states each individual interacts with at least one other. Nevertheless, the growth relationship of separate individuals

$$\alpha_i = \frac{\lambda}{K_i}, \quad i \in \{1, 2, \dots, n\}$$

holds with  $K_i$ , denoting *weight*, at *sexual maturity of the  $i$ th individual*. Of course, the  $K$ 's are carrying capacities for the  $n$  Formal Modular Populations, the FMP.

There are interesting consequences from this model:

- (1) Rate of change of weight,  $F$ , increases that rate for every other fish, because of  $F^2$  terms which indicate reproductive activity between individuals. The male or female designation is dropped entirely in AMD.
- (2) There can be no third party interactions. For example, Stickleback spawning or nesting interactions: two females cannot spawn into the same nest, nor can two males “gang up” on a third, keeping him from nesting.
- (3) All individuals within a school are competing for food and other resources. For example, in Sticklebacks there is competition to build nests among males while females compete to spawn into a particular nest.

Further information known for the production space geometry, [10], [2], [8], [6], indicate:

- (4) School biomass production trajectories (paths in production space) diverge so that production is chaotic. This tendency diminishes asymptotically to zero, as time goes to infinity. This follows from the negativity of the Riemann Scalar curvature  $R$ , in, (3.6) below. Such social behavior has been termed: *vigorous*. The tendency is for vigor to diminish over time. The more negative is the curvature,  $R$ , at a particular state,  $(y_1, y_2, \dots, y_n)$ , the more vigorous the behavior.

- (5) Trajectories become asymptotically unidirectional in the direction determined by  $(\alpha_1, \alpha_2, \dots, \alpha_n) = \vec{\alpha}$  through the ratios,  $\alpha_i/\alpha_j$ , the production system decouples asymptotically to one where each fish acts completely independent of all others. Thus, for large times, a school is no longer coherent because there are no more social interactions, [2], [10].

**Remark.** If we interpret the equations, (3.2) through (3.5), as referring to a feeding school, then the divergent (chaotic) behaviour early on, gradually diminishes, presumably because each fish has eaten its fill.

Production (i.e., Jacobi) stability is determined by the Riemann scalar curvature,  $R$ , of (3.4). In terms of natural coordinates  $(y_1, y_2, \dots, y_n)$ , it is found to be:

$$R = -(n-1)(n-2)[\alpha_1^2 + \alpha_2^2 + \dots + \alpha_n^2]e^{-2\alpha y^i},$$

which is negative, if  $n$  is at least 3, and vanishing when  $n = 2$ , [2], [8]. As stated in (4), this means trajectories diverge so that production is chaotic. This is not a bad thing. It allows the school to react fast to changing conditions and reflects the school's opportunistic role in their growth and survival. Because  $F$ 's are always positive, the  $y$ 's must be increasing with time, so that,  $R \nearrow 0$  asymptotically. Consequently, production of any surrogate becomes steadily less chaotic.

For comparison, the (Jacobi) stability index of system (1.2) with vanishing  $\varepsilon$  is:

$$R = \frac{\lambda^2}{\lambda+1} v \left( \frac{F^1}{F^2} \right)^{1+2/\lambda} e^{-2Q(y)}, \quad (3.6)$$

with  $Q(y)$  given by (1.6). Note that  $R$  is positive so production/reproduction is (Jacobi) stable for (1.2).

**Remark.** In a model with noise added to (3.2), the mean time until first exit from any fixed simply connected compact region in  $T\Omega$  is smaller compared to a flat space (Euclidean) Brownian motion. Thus, the influence of the negative scalar curvature,  $R$ , is to speed-up sample paths of the noisy production process, [3], [9], [11]. This means a school of fish is able to take quicker advantage of contingencies which occur in its ambient environment, and so enhances joint production (or consumption).

Let's look at the School Equations for  $n = 3$ : We use the Volterra Production Equation in (1.2), together with:

$$\frac{dF^1}{dt} = -\alpha_1(F^1)^2 + \alpha_1[(F^2)^2 + (F^3)^2] - 2F^1[\alpha_2F^2 + \alpha_3F^3] + \lambda F^1$$

$$\begin{aligned}\frac{dF^2}{dt} &= -\alpha_2(F^2)^2 + \alpha_2[(F^3)^2 + (F^1)^2] - 2F^2[\alpha_1F^1 + \alpha_3F^3] + \lambda F^2 \\ (3.7) \\ \frac{dF^3}{dt} &= -\alpha_3(F^3)^2 + \alpha_3[(F^1)^2 + (F^2)^2] - 2F^3[\alpha_1F^1 + \alpha_2F^2] + \lambda F^3\end{aligned}$$

The equilibrium for (3.2) through (3.5) and (3.7) is stable and is the unique positive one, for  $n$  individuals ( $n = 3$ , in this case),

$$F_*^i = \frac{\lambda \alpha_i}{\|\vec{\alpha}\|^2}, \quad i \in \{1, 2, \dots, n\}.$$

The vertical double bar indicates the Euclidean norm of vector  $\vec{\alpha}$ . These steady-state values are completely determined by  $K_i$ , the  $i$ th *weight* (or scaled size) at sexual maturity, since for each index value,  $j$ , equation (3.5) holds, so that  $\lambda$  cancels out.

Note: the sign of the linear term in (3.7) has changed from  $-$  to  $+$  due to using the total production variable,  $X$ , instead of the net growth variable,  $y$ .

**Question:** What effect does unbiased predation, including balanced exploitation by humans, have on a school?

When a BE term is added to (3.7), does it yield a new asymptotic direction ( i.e., steady-state ratios) in production space? The answer is NO. But, the steady-state values,  $F_*^i$ , do change. The case of arbitrary  $n$  is given by

**Theorem C.** *Weight Ratios at equilibrium,  $F_*^i/F_*^j$ ,  $i \neq j$ , with  $i, j \in \{1, 2, \dots, n\}$ , are unchanged under balanced exploitation, but the  $n$  new steady-state values,  $F_*^k$ , depend on  $\{e_i\}$  and are smaller valued.*

In order to help understand this result, look at the BE- equations for the  $n = 3$  of system (3.7):

$$\begin{aligned}\frac{dF^1}{dt} &= -(\alpha_1 + e_1)(F^1)^2 + \alpha_1[(F^2)^2 + (F^3)^2] - (2\alpha_2 + e_2)F^1F^2 - (2\alpha_3 + e_3)F^1F^3 + \lambda F^1, \\ \frac{d^2F^2}{dt^2} &= -(\alpha_2 + e_2)(F^2)^2 + \alpha_2[(F^1)^2 + (F^3)^2] - (2\alpha_1 + e_1)F^2F^1 - (2\alpha_3 + e_3)F^2F^3 + \lambda F^2, \\ \frac{d^2F^3}{dt^2} &= -(\alpha_3 + e_3)(F^3)^2 + \alpha_3[(F^1)^2 + (F^2)^2] - (2\alpha_3 + e_3)F^2F^3 - (2\alpha_1 + e_1)F^3F^1 + \lambda F^3.\end{aligned}$$

An exercise for the reader: Compute the steady-state  $F$ -values and their ratios in order to verify the theorem for  $n = 3$ . The proof in the general case is the same.

Your Conclusion: BE forces the *weight* at steady-state to be smaller per individual, but the every *weight ratio* is unchanged.

**Open problems.** Determine the production stability for the two systems above after BE has been applied. Determine the maximum sustainable yield for the shoal model with  $n$  individuals.

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