# A POLARITY-ENERGY FOOD CHAIN TROPHIC CASCADE MODEL: IMPLICATIONS TO FISHERY MANAGEMENT

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***Abstract***

*The paper developed a model that extends the classical Oksanen Polarity Theorem for simple food chains to accommodate the analyses of energy transfers from one trophic level to another. The Polarity-Energy Food Chain Trophic Cascade model developed is then used in the analysis of data obtained by researchers for sardines (Sardinella lemuru) and lake herring (Coregonous artedii). Results revealed that for the sardine population in the east coast of Siberut Island, a stable logistic population growth is observed. These information means that population of this pelagic fish species increases (as a function of time n) until it reaches a stable population if left on its own based on the logistic growth hypothesis. However, over-predation by the top level consumer (over-fishing) can disrupt this approach to stability (i.e. fishing intensity of $\delta > 14.5\%$) or if fish larvae are caught by very fine gill nets (i.e. causing a reduction in the value of r). Fishery closure during spawning period (September to October) up to March or April each year ensures sustainable catch for this fish species. On the other hand, for the population of lake herring in the Great Lakes displayed large fluctuations in both yield and effort. Data tend to support a growth rate $r > 3.5$ if a logistic growth model were used because of the observed chaotic fluctuations. This means that fishing has caused a decreased in fecundity (as reported) leading to a greater value of the growth rate r (ratio of average eggs per female to fecundity). Overall, the Polarity-Energy Food Chain Model developed supports temporary fishing ban or permanent identification of marine protected areas (MPA) to preserve the natural logistic growth patterns of economically-important fish species. In the former case, fishing is timed with the observed population periodicities while in the latter case, fishing can be allowed outside of the protected area which benefits from spill-over effects of the MPA.*

***Keywords:*** *trophic cascades, food chains, food web, trophic levels, filter nets*

## 1.0 Introduction

Trophic cascades occur when predators in a food chain or web suppress the abundance and/or alter traits of their prey, thereby releasing the next lower tropic level from predation (Carpenter et al., 1985). A Top-Down Cascade is a trophic cascade where the food chain or food web is disrupted by the removal of a top predator, or a third or fourth level consumer. On the other hand, a bottom up cascades occurs when a primary producer, or primary consumer is removed, and there is a decrease of population size through the community (Beschta & Ripple, 2009). Hairston, Smith and Slobodkin (1960) argued that predators reduce the abundance of herbivores, allowing plants to flourish. This is often referred to as the green world hypothesis. The green world hypothesis is credited with bringing attention to the role of

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top-down forces (e.g.predation) and indirect effects in shaping ecological communities. According to Oksanen et al., (1981), a trophic level in food chain increases the abundance of producers in food chains with odd number of trophic levels, but decreases the abundance of the producers in food chains with an even number of trophic levels. Additionally, he argued that the number of trophic levels in a food chain increases as the productivity of the ecosystem increases. This paper modifies Oksanen's et al., (1981) polarity model for linear food chains to include biomass transfers from one trophic level to the next. Additionally, the paper also examines the compatibility of existing fishery management practices e.g. temporary fishing bans and establishment of marine protected areas (MPA) as espoused by Russ & Alcala (1996), with the predictions derived from the model.

Existing models for trophic cascades such as those of Hairston, Smith and Slobodkin (1960) and Oksanen (1981) deal with linear food chains. Extensions in the case of food webs have been made using extensive simulation models (ECOSIM) by Pauly et al. (2000) but non-computer based mathematical models have not been fully developed. Mathematical models such as the one proposed in this study are useful for prediction and scenario analysis. In turn, prediction and scenario models are important bases for fishery policy. Section 2 reviews the formulation of the classical cascade model of Oksanen et al., (1981) and extends the results to biomass changes at each trophic level. Section 3 uses the model to analyze the periodicities of populations at the lower trophic levels of the food chain; real-life illustrative examples are also provided in this section. Finally, Section 4 gives the conclusions drawn from the model and the analysis of real-life situations.

## 2.0 Linear Food Chain Trophic Cascade Model

A linear food chain representation is given below. The number of functional trophic levels are often inferred from the literature available on resource and ecological assessment surveys conducted in the area.

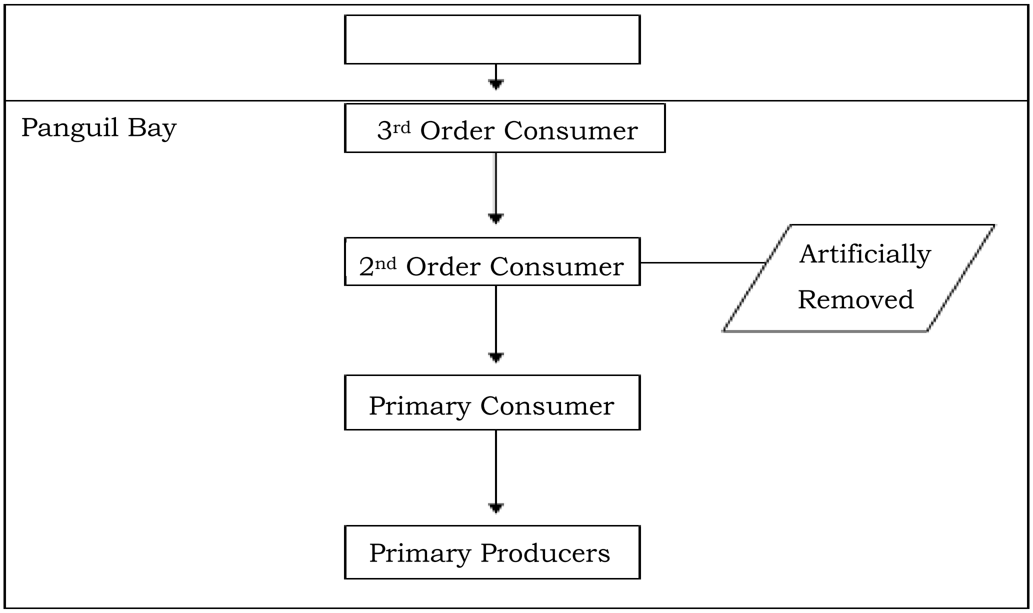

Figure 1. Linear food chain model

Oksanen (1981) stated that:

**Theorem (Oksanen, 1981).** If there are odd number of functional trophic levels, then an increase (+) in the topmost level will induce an increase (+) in the primary producers ; if there are an even number of trophic levels, then the same phenomenon will induce a decrease (-) of the primary producers. **Proof:** Let k = 2n+1, ne$Z^+$ be the number of trophic levels. Starting from the topmost level we obtain a sequence of plus (+) and minus polarities: (+,-,+,-,...,+). Let $p = (-1)^{k-1}$ be a polarity function. Substituting the value of k = 2n+1, we obtain: $p = (-1)^{2n}$ or $p = +1$ polarity. The same proof works when k = 2n.

## Polarity-Energy Food Chain Trophic Cascade model

We attempt to enhance the practical use of this theorem by considering the energy transfers (biomass conversions) from one trophic level to the next. The following assumptions are needed in order to develop the model:

**Assumptions:**

1. An organism in trophic level $T_{j-1}$ predates on organisms in trophic level $T_j$ , j =1,2,...,k
2. If there are $n_j$ organisms in trophic level $T_j$, then the organisms in trophic level $T_{j-1}$ requires $\alpha_j(n_j)$ preys in order to reproduce. The constants $\alpha_j$ are called predation constants.
3. Increases in the number of organisms at each trophic level, except for the topmost consumers, are determined by the forces of predation, reproduction, and natural mortality. The number of topmost consumers are determined by several other factors, all of which are summarized in the quantity $\Delta n_1$.
4. Changes in the population sizes at each trophic level are determined by a density-dependent population growth model which incorporates the forces of birth-death.
5. An ecosystem is in equilibrium if $n_1 < n_2 < n_3 < \ldots < n_k$

It is convenient to discuss the density-dependent population growth model assumed in (4) because this will be used in the development of the model. Let p(n) be the population at a particular trophic level at time n, the simplest model for p(n) is to assume that the population change is proportional to the number present:

$$p(n+1) - p(n) = rp(n),$$

where r is the constant of proportionality.

This equation means that $p(n+1) = (1+r)p(n)$ with $p(0) = p_0$ , whose solution is easily found to be: $p(n) = (1+r)^n p_0$. The main problem with this population model is that it assumes that the environment has infinite resources to support growth. A more realistic model is to assume that the environment has a finite carrying capacity (say, c). From:

$$p(n+1) - p(n) = rp(n)$$

we curb population growth by inputting the carrying capacity of the environment:

$$p(n+1) - p(n) = rp(n)[c-p(n)].$$

Note that there will be zero population growth once the population p(n) reaches the maximum carrying capacity (c) of the environment. This logistic population growth model reduces to:

1. $p(n+1) = (1+rc)p(n)\left[1 - \frac{r}{1+rc}\, p(n)\right]$
2. $a(n) = \frac{r}{1+rc}\, p(n)$

to obtain the final model:

3. $a(n+1) = \rho\alpha(n)\,[1-\alpha(n)]$

where: $\rho = 1 + rc$.

Since for each n, $p(n) \le c$, it follows that (2) is a normalized population growth model, that is, $0 \le a(n) \le 1$. The initial population ( i.e. population at time of first observation) is assumed known, $a(0) = a_0$. Likewise, we assume that $r > 0$, so that the $\rho > 1$. Model (2) exhibits many different types of behavior of population growths: (a) for $0 < \rho < 2.8$, steady state; (b) for $2.8 < \rho \le 3.3$, two-value cycle; (c) for $3.3 < \rho \le 3.55$, four-value cycle; (d) for $\rho \ge 3.829$, chaos. We illustrate the logistic model fit for the Philippine population data as shown in Table 1.

Table 1. Philippine population data from year 1903-2010

| **Year** | **Population** | **± % p.a** |
|---|---|---|
| 1903 | 7635426 | — |
| 1918 | 10314310 | 2.03 |
| 1939 | 16000303 | 2.11 |
| 1948 | 19234182 | 2.07 |
| 1960 | 27087685 | 2.89 |
| 1970 | 36684486 | 3.08 |
| 1975 | 42070660 | 2.78 |
| 1980 | 48098460 | 2.71 |
| 1990 | 60703206 | 2.35 |
| 1995 | 68616536 | 2.48 |
| 2000 | 76498735 | 2.20 |
| 2007 | 88574614 | 2.12 |
| 2010 | 92337852 | 1.40 |

Source: NSO, 2013

The value of r is computed from $p(n+1) - p(n) = rp(n)$ by first dividing the difference $p(n+1) - p(n)$ by the time difference between censuses. This gives an approximate value for the "annual" population difference. The result is then divided by p(n) to obtain r. The results are tabulated value in Table 2.

The graph of the difference $(p(n+1)-p(n))$ versus p(n) is shown in figure 1. We are observing a two-cycle regime for the Philippine population and so it is possible that $2.8<\rho\le3.3$. If we are close to $\rho = 3.3$, then given the observed value of r, we can infer the Philippine maximum carrying capacity to be:

$$3.3 = 1 + .01934{*}c \rightarrow c = 118{,}924{,}510 \text{ people}$$

which further means that if the population grows at 1,000,000 per annum, then the maximum carrying capacity is reached in 25 years (estimated Philippine

Table 2. Computed estimation of *r*

| Year | Population | ± % p.a | diff/time | r |
|---|---|---|---|---|
| 1903 | 7635426 | — | 0 | 0 |
| 1918 | 10314310 | 2.03 | 178592 | 0.017315 |
| 1939 | 16000303 | 2.11 | 270762 | 0.016922 |
| 1948 | 19234182 | 2.07 | 359320 | 0.018681 |
| 1960 | 27087685 | 2.89 | 654459 | 0.024161 |
| 1970 | 36684486 | 3.08 | 959680 | 0.02616 |
| 1975 | 42070660 | 2.78 | 1077235 | 0.025605 |
| 1980 | 48098460 | 2.71 | 1205560 | 0.025064 |
| 1990 | 60703206 | 2.35 | 1260475 | 0.020765 |
| 1995 | 68616536 | 2.48 | 1582666 | 0.023065 |
| 2000 | 76498735 | 2.20 | 1576440 | 0.020607 |
| 2007 | 88574614 | 2.12 | 1725126 | 0.019477 |
| 2010 | 92337852 | 1.40 | 1254413 | 0.013585 |
| | | | **Average value of r:** | **r = 0.01934** |

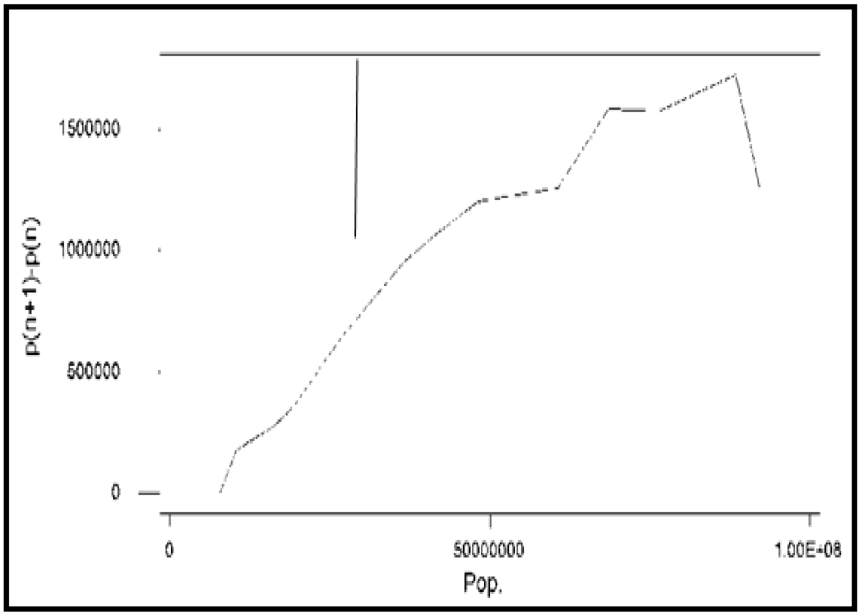

Figure 2. Philippine relative population change

Population in 2012 was 94,000,000) i.e. in year 2039. Close to this maximum carrying capacity, the Philippine population will begin to exhibit a four-period cycle. The two-period cycle observed in Figure 1 began after a consistent upward movement in Philippine population. Periods of "booms" and "busts" last for approximately 3 years (population stays at a certain level for 3 years and then shifts either downward or upward).

The logistic growth model considers only the natural forces of birth and natural mortality in the context of a limited-resource environment (maximum carrying capacity).

## Trophic Cascade Model for Food Chains

Let $T = 3$ trophic levels. Assume that the topmost consumer increased from $p_1(n)$ to $p_1(n) + \delta p_1(n)$ at time n. Using Oksanen's et al., (1981) result we obtain the series of inequalities based on the equilibrium condition:

$$p_1(n) + \delta p_1(n) < p_2(n) - \alpha_2[p_1(n) + \delta p_1(n)] < p_3(n) + \alpha_3[-p_2(n) + \alpha_2(p_1(n) + \delta p_1(n))]$$

Note that the signs (+ or -) are determined based on the polarity theorem of Oksanen. From this condition, we obtain the necessary predation rates for equilibrium:

$$1.\ \alpha_2 < \frac{p_2(n)}{p_1(n) + p_1(n)\delta} - 1$$

$$2.\ \alpha_3 < \frac{p_3(n)}{p_1(n) + p_1(n)\delta} - 1$$

The denominator can be simplified to $(1+\delta)\ p_1(n)$ so the predation rates for equilibrium become:

$$3.\ \alpha_2 < \frac{p_2(n)}{(1+\delta)p_1(n)} - 1$$

$$\alpha_3 < \frac{p_3(n)}{(1+\delta)p_1(n)} - 1$$

If there is population stability in the long run, then it can be shown that:

$$p_j(n) \to \frac{\rho_j - 1}{\rho_j} \text{ as } n \to \infty$$

Suppose that the populations attains stability ($1 < \rho < 2.8$), then we can compute the asymptotic predation rates as follows:

$$4.\ \alpha_2 < \frac{\rho_2 - 1}{\rho_2} \ \frac{(1+\delta)\rho_1 - 1}{(1+\delta)\rho_1} - 1$$

$$5.\ \alpha_3 < \frac{\rho_3 - 1}{\rho_3} \ \frac{(1+\delta)\rho_1 - 1}{(1+\delta)\rho_1} - 1$$

For illustration purposes, assume that $\rho_1 = 2$, $\rho_2 = 2.5$, and $\delta = .05$, $a_1(0) = .45$, $a_2(0) = .55$, and compute the asymptotic predation rate $\alpha_2$ as shown in table 3:

Table 3. Asymptotic predation rate

| **$\rho_1$ (n)** | **$\rho_2$(n)** | **$\alpha_2$** | **Iteration no.** |
|---|---|---|---|
| 0.52381 | 0.6 | 0.145454258 | 20 |
| 0.52381 | 0.6 | 0.145454689 | 21 |
| 0.52381 | 0.6 | 0.145454473 | 22 |
| 0.52381 | 0.6 | 0.145454581 | 23 |
| 0.52381 | 0.6 | 0.145454527 | 24 |
| 0.52381 | 0.6 | 0.145454554 | 25 |
| 0.52381 | 0.6 | 0.145454541 | 26 |
| 0.52381 | 0.6 | 0.145454548 | 27 |
| 0.52381 | 0.6 | 0.145454544 | 28 |
| 0.52381 | 0.6 | 0.145454546 | 29 |
| 0.52381 | 0.6 | 0.145454545 | 30 |

Thus, given the population increase at the topmost consumer (at $\delta$ = 5%) and a stable population logistic growth model at the lower trophic level, then the predation rate must be below 14.5% in order to maintain Oksanen's et al., (1981) polarity theorem which assumes the equilibrium condition. This relates to the Ten-Percent Law in Ecology (Lindeman, 1942 as cited by Cook, 1977).

Energy transfer between trophic levels is inefficient, such that net production at one trophic level is generally only 10% of the net production at the preceding trophic level. Due to non-predatory death, egestion, and respiration, a significant amount of energy is lost to the environment instead of being absorbed for production by consumers. The 10%-figure approximates the fraction of energy available after each stage of energy loss in a typical ecosystem, although these fractions vary greatly from ecosystem to ecosystem and from trophic level to trophic level. The loss of energy by a factor of one half from each of the steps of non-predatory death, defecation, and respiration is typical of many living systems. Thus, the net production at one trophic level is or approximately ten percent that of the trophic level before it. This implies that if the predation rate is maintained at the 10% level, then the equilibrium condition used in Oksanen's (1981) theorem is satisfied.

### Increase in Top Consumers (More Fishers and More Efficient Fishing Gears)

The optimal predation rates given an increase in the number of top level consumers depends on the value of $\delta$ which may not be fixed for all time n. It is logical, in fact, to assume that this increases as a function of time i.e. more fishers, more efficient fishing gears, because of human population pressure. We ask for the limit of this increase in δ beyond which the equilibrium condition of Oksanen et al., (1981) will be violated i.e. the limit in the increase of human predation. Setting (4) equal to zero yields:

$$6.\ \delta = \frac{\rho_2 - \rho_1}{\rho_2}$$

## 3.0 Trophic Cascade Model for Food Chain With Periodic Population Cycles

The logistic population growth model used in the previous section displays a wide array of long-term behavior. We discuss these dynamic behavior by considering the logistic map:

$$f(x) = rx\,(1-x),\ r > 0$$

A point x is said to be a **fixed point** of the map if x = f(x). If the growth rate r is between 0 and 1, then the only fixed point is x = 0, in which case, the population ultimately becomes extinct. If the growth rate is between 1 and 3, the logistic map has two fixed points, namely, x = 0 (which is a **repelling** fixed point) and x = (r-1)/r (which is an **attracting** fixed point). The case considered in the previous section was of this type where the populations ultimately become stable. Under this regime, the population increases from x = 0 to its stable fixed point (r-1)/r.

The Philippine population data reveals yet another possibility where r > 3. In this case, both the original fixed points are repelling while the other two are attracting periodic points.

Solving $f^2(x) = x$ gives us four roots

$$x = 0$$

$$x = 1 - 1/r,$$

$$x = \frac{r + 1 \pm\sqrt{(r-3)\,(r+1)}}{2r}$$

The first two are clearly the repelling fixed points. The second two are two-periodic points.

When $x_0 = \frac{r+1 \pm \sqrt{(r-3)\,(r+1)}}{2r}$, $(f^2)'(x_0) = 4 + 2r - r^2$. Therefore, the 2-cycle is attracting for $4 + 2r - r^2 < 1$ i.e. $3 < r < 1 + \sqrt{6} \approx 3.449...$ A graphical illustration when r = 3.1, $a_0$ = .45 is shown below:

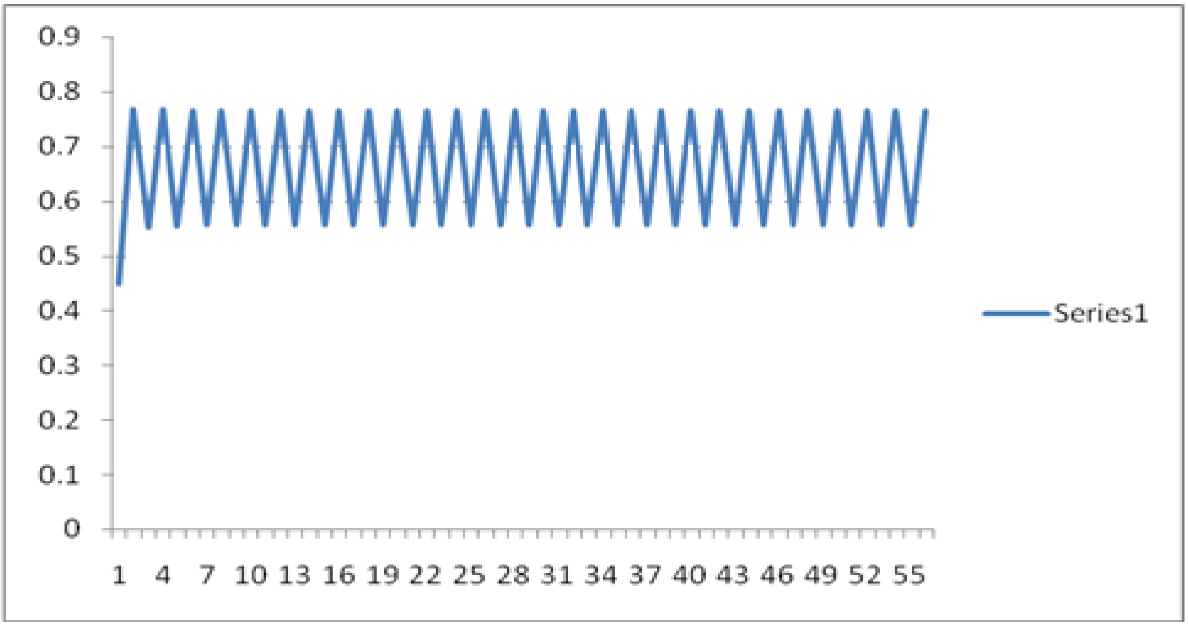

Figure 4. Two-cycle population growth with attracting fixed points: x = .76 and x = .56

When the growth parameter *r* exceeds 3.449, the population undergoes a series of bifurcations (4-period, 8-period, $2^n$-period) resulting in ultimate chaos. These population changes hold true at all trophic levels in a food chain and can be used as a basis for fishery policies.

**Real Illustrative Example 1.** The study of Ginanjar (2006) suggests that the pelagic fish *Sardinella lemuru* has a growth parameter not exceeding r = 2.81 (based on the ratio of egg production per female (max:=22) and fecundity (7.85), hence, estimated r = 22/7.85 = 2.803). Spawning period was observed to be between the months of September and October and that no evidence was found that *S. lemuru* spawn more than one time a year. These information means that that population of this pelagic fish species increases (as a function of time n) until it reaches a stable population if left on its own based on the logistic growth hypothesis. However, over-predation by the top level consumer (over-fishing) can disrupt this approach to stability ( i.e. $\delta > 14.5\%$) or if fish larvae are caught by very fine gill nets (i.e. reduction in the value of r). *Fishery closure during spawning period (September to October) up to March or April each year ensures sustainable catch for this fish species.* In August, 2013, such a ban for fishing sardines in the Zamboanga Peninsula area was, in fact, announced.

**Real Illustrative Example 2.** Jensen (1984) observed the various behaviors of fish populations, specifically looking into the observed yield of lake herring (*Coregonus* *artedii*) from the upper Great Lakes. Conventional surplus production models assume that fisheries do not impact the population's capacity to increase, but changes in age structure or a decrease in age-specific fecundity resulting from fishing can decrease the coefficient of increase. A surplus production model is developed in which fishing reduces the capacity of a population to increase; the model is applied to describe the fluctuations observed in yield of lake herring (*Coregonus artedii*) from the upper Great Lakes. The fisheries of the Great Lakes were decimated by the combined effects of heavy fishing and a changing environment. For some species, yield increased to high levels and then the fisheries collapsed; for other species, yield and effort fluctuated greatly. If a logistic growth model were used in Jensen's study (1984), the high fluctuations in both yield and effort could be explained by a growth rate r > 3.5 i.e. decrease in fecundity (observed by Jensen, 1984), which appears in the denominator, increases r, thus, explaining the chaotic behavior of yields of lake herring.

## 4.0 Conclusion

The analyses performed serve to illustrate the usefulness of modelling fish population dynamics through the logistic growth model as it accommodates many possibilities for the fish population growth. For instance, conventional surplus production models indicate that destruction of fish populations by overfishing is difficult, if not impossible, but *catastrophic declines in abundance of exploited populations are common.* Surplus production models also do not predict large continuing fluctuations in yield, but *large fluctuations in yield are common.* Likewise, the logistic growth model contains the parameter *r* which can be easily estimated through gonadal somatic index (Ginanjar, 2006). The effects of top predation (over-fishing) on the lower trophic levels on the value of *r* can then be more clearly gleaned.

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